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Les amphibiens et reptiles du Miocène supérieur et du Pliocène inférieur de la région de Ptolémaïs (Macédoine occidentale, Grèce)

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ABSTRACT

We herein describe the amphibians and reptiles from the Ptolemais fossil assemblage, originating from 12 nearby localities in northwestern Greece, spanning from the late Miocene (MN 13) to the early Pliocene (MN 15). Amphibians are known exclusively of anurans, with the genera *Latonia* and *Rana* being identified, the latter constituting the oldest so far known record of that lineage in Greece. Turtles are represented by the testudinid cf. *Testudo*, whereas numerous other indeterminate testudinoids are known. Lizards include scincids, lacertids, and at least two anguids. Among them, the material referred to scincids and the anguid *Anguis* constitute one of only rather few such occurrences described in the fossil record of the Eastern Mediterranean. Snakes are represented by indeterminate "colubrines" and the genus *Natrix*. The different ages of the Ptolemais fossiliferous localities, along with their close geographic vicinity offer the opportunity to study potential survival / extinction patterns of its amphibians and reptiles across the Mio-Pliocene boundary, a time interval that has been crucial for European herpetofaunas.

Keywords: Amphibians; Testudines; Squamata; Neogene; Greece

RÉSUMÉ

Nous décrivons ici les amphibiens et reptiles provenant de l'assemblage fossile de Ptolémaïs, issus de 12 localités géographiquement proches au nord-ouest de la Grèce, couvrant une période allant du Miocène supérieur (MN 13) au Pliocène inférieur (MN 15). Les amphibiens sont uniquement représentés par des anoures, dont les genres identifiés sont *Latonia* et *Rana.* La présence de ce dernier constitue la plus ancienne occurrence connue à l'heure actuelle en Grèce. Les tortues sont représentées par cf. *Testudo,* bien que plusieurs restes indéterminés de testudinoïdes soient connus. Les lézards comprennent des scincidés, des lacertidés et au moins deux anguidés. Chez les lézards, le matériel référé aux scincidés ainsi que l'anguidé *Anguis* constituent l'une des quelques occurrences éparses connues dans le registre fossile de l'Est de la Méditerranée. Les serpents sont représentés par des « colubrines » indéterminés et le genre *Natrix*. Les différents âges des localités fossilifères de Ptolémaïs, associés à la proximité géographique de ces dernières, offrent l'opportunité d'étudier les modèles potentiels de survie / extinction des amphibiens et des reptiles autour de la limite Mio-Pliocène, une période cruciale pour les herpétofaunes européennes.

Mots clés : Amphibiens ; Reptiles ; Néogène ; Grèce

1. Introduction

Studies of Neogene and Quaternary amphibians and reptiles from Europe have traditionally not attracted the attention of palaeontologists to the same extent as other vertebrate clades, mammals in particular, and nearly all the localities that yielded micro- and macrovertebrates were explored with the main goal of collecting mammals for taxonomic, biostratigraphic and palaeobiogeographic reasons. The retrieval of fossil amphibians and reptiles is therefore generally a byproduct of the quest for mammals. However, in the last few decades a rising interest in European palaeoherpetofaunas significantly improved our knowledge of the recent evolution of the amphibian and reptile assemblages (among others: Rage and Roček, 2003; Szyndlar, 2012; Roček, 2013; Villa and Delfino, 2018). Studies dedicated to the amphibians and reptiles of the Balkan Peninsula followed chronologically those on Western and Central European localities and, with few exceptions (see for example Đurić, 2016; Vasilyan, 2019), deal almost exclusively with Greek materials (Georgalis and Kear, 2013; Georgalis et al.,2013, 2016a, 2016b, 2016c, 2017, 2018a, 2018b, 2019a, b;

Vlachos et al., 2015, 2019; Vlachos and Delfino, 2016) also thanks to the fact that a significant collection of Greek fossil microvertebrates has been put together in the 1970's, 1980's, and 1990's by the research team of the Department of Earth Sciences of the University of Utrecht (The Netherlands), at certain times also in collaboration with the National and Kapodistrian University of Athens (Greece).

The intramontane Florina-Ptolemais-Servia Basin in Western Macedonia, in northern Greece, is one of the areas investigated by the above-mentioned researchers. This Basin has been known and exploited for its abundant lignite resources for several decades. Indeed, northwestern Greece is the home of more than two thirds of the total lignite supplies of the country (Kalaitzidis et al., 2004). From a palaeontological point of view, the Ptolemais Basin has yielded numerous micromammals (Hordijk and de Bruijn, 2009) and was the subject of several publications in the last decades (Steenbrink et al., 1999, 2006; Kalaitzidis et al., 2004; Kloosterboer-van Hoeve et al., 2006). However, no amphibian or reptile remains have ever been described.

This paper presents the amphibians and reptiles findings from the 12 late Miocene (Messinian, MN 13) to early Pliocene (Zanclean, MN15) lignitiferous localities of the Ptolemais Basin. The vast majority of this material can only be identified to high taxonomic levels due to its highly fragmented nature. However, genus-level identification was achieved for at least part of the material.

2. Geological and palaeoecological settings

The material presented in this study comes from 12 localities of the Ptolemais Basin, each of them being an open-pit lignite mine. In this area, mining exploitations are still in activity. This Basin belongs to the larger intramontane Florina-Ptolemais-Servia Basin that extends from the borders of the Former Yugoslav Republic of Macedonia to the city of Kozani, northwestern Greece (Fig. 1). This geologic structure is a 120km long tectonic trench with a NNW-SSE direction. The Florina-Ptolemais-Servia Basin can be subdivided in two sub-basins: the Servia sub-basin and the Ptolemais sub-basin (Steenbrink et al., 1999, 2006), which is commonly referred as the Ptolemais Basin.

The herein described material was recovered in several lignite levels that are exposed in 12 outcrops found in four different localities of the Florina-Ptolemais-Servia Basin. These localities are the open-pit quarries of Tomea Eksi, Komanos, Vorio and Notio. The outcrops are Tomea Eksi 1, Tomea Eksi 2 and Komanos 1 (pertaining to the MN 13 zone), Vorio 1 and Vorio 2 (pertaining to the late MN 14 zone), Tomea Eksi 3, Vorio 3, Vorio 3A, Vorio 4, Vorio 8 and Notio 1 (from the MN 15 zone). Detailed descriptions and the age calibrations of these localities are provided by Hordijk and de Bruijn (2009). In the rest of the text and in the collection numbers of the specimens, these localities are referred respectively as TE1, TE2, KO1lowB and KO1highA, VOR1, VOR2, TE3, VOR3, VOR3A, VOR4, VOR8, and NO1. The lignite bed of Komanos contains two distinct erosional surfaces that are marked by lateral variation. The letters A and B refer to a lateral distance of 50 meters between two sampling sites pertaining to the same layer and the qualifiers “low” and “high” refer to the different erosional surfaces. The original purpose of the distinction between these outcrops was to obtain information about any lateral variation in the composition of the mammalian fauna studied by Hordijk and de Bruijn (2009). The 12 outcrops were used to produce a general composite section of the whole basin (Steenbrink et al., 1999). The sedimentology of the basin is characterized by lacustrine marls in which several ash layers, fluvial deposits and lignite layers are intercalated (Steenbrink et al., 2006; Hordijk and de Bruijn, 2009). The Ptolemais Basin is currently relatively well known thanks to studies in diverse disciplines that were conducted in the last decades: sedimentology, cyclostratigraphy, magnetostratigraphy, isotopic analysis, micromammal palaeontology, palynology, palaeobotany and palaeoenvironmental reconstruction (Kalaitzidis et al., 2004; Kloosterboer-van Hoeve et al., 2006; Steenbrink et al., 2006; Hordijk and de Bruijn, 2009). For a more detailed description of the geology of the Basin and its depositional history, the reader is referred to Steenbrink et al. (1999, 2000, 2006).

The oldest localities (TE1 and TE2) belong to the Tomea Eksi member of the Komnina Formation, which itself represents the youngest deposits of the latter. They were respectively dated to a time interval comprised between 5.32 and 5.43 Ma and between 5.30 and 5.40 Ma. The lithology of this member is characterized by rhythmic deposits of fine sediments alternating between diatomaceous marls of lacustrine origin and lignite accumulations. These lignite levels are composed of xylite (Steenbrink et al., 2006). The Komnina Formation was dated to the late Miocene (and eventually early Pliocene for its uppermost portion) on the basis of palaeontological remains (micromammals; Hordijk and de Bruijn, 2009) and both magneto- and cyclostratigraphic analyses (Steenbrink et al., 2000). The other, younger, localities of Komanos (KO1lowB and KO1highA), Vorio (VOR1 to VOR8) and Tomea Eksi (TE3) pertain to the Kyrio member. The latter is the oldest member of the Ptolemais Formation and is followed by the Theodoxus member and the Notio member. The sedimentology is here characterized by thick grey marls with intercalation of xylite-rich lignite accumulation levels, which are rhythmically bedded (Hordijk and de Bruijn, 2009). The oldest sediments of the Ptolemais Formation (i.e., outcrops of KO1) were dated to 5.25 Ma on the basis of isotopic analyses and astronomical calibration. The sediments from Vorio 1 were dated to 5.04 Ma. The sediments from Tomea Eksi 3 were dated to a time interval comprised between 4.93 and 4.97 Ma. The sediments from Vorio 3 and Vorio 3A were dated to 4.9 Ma. The youngest sediments of this formation (i.e., outcrop of NO1) were dated to 3.94

Ma (Van Vugt et al., 1998; Steenbrink et al., 2006). The precise age of Vorio 2, Vorio 4 and Vorio 8 is not known.

Previous studies performed in the Florina-Ptolemais-Servia Basin highlighted the presence of a diversified microvertebrate fauna, mainly dominated by murid rodents, accompanied also by sciurids, castorids, cricetids, pteromyd glirids and lagomorphs (Hordijk and de Bruijn, 2009). Large-sized mammals are only poorly documented. So far, they include primate and rhinocerotid remains (Hordijk and de Bruijn, 2009). This mammal fauna is also associated with several invertebrate taxa such as ostracods and gastropods (Steenbrink et al., 1999, 2006) or dinoflagellates (Kloosterboer-van Hoeve et al., 2001). The Pliocene flora of the Florina-Ptolemais-Servia Basin has also been examined. The autochthonous vegetation assemblage contains a variety of arboreal and herbaceous angiosperm taxa and a few Taxodiaceae and Pinaceae conifers (Kalaitzidis et al., 2004; Kloosterboer-van Hoeve et al., 2006). Moreover, the presence of algae and fungal remains was mentioned in the area (Steenbrink et al., 1999; Kloosterboer-van Hoeve et al., 2001, 2006).

Palynological analyses have shown that the palaeoenvironment and vegetation in which the Tomea Eksi member late deposits occurred were subject to a major shift due to variations in precipitations (Kloosterboer-van Hoeve, 2000). Moreover, the deposits of the Ptolemais Formation and its lignite accumulation are typical of shallow-lacustrine sedimentation under relatively dry conditions (Steenbrink et al., 1999, 2006). The late part of the Ptolemais Formation is characterized by its xylite-rich lignite and is referred to as the "Upper Xylite Layer" by Kalaitzidis et al. (2004). It has been shown that these particular deposits were produced by local wet forest fens or forest swamps and accumulated near a lake under limnotelmatic to telmatic conditions associated to a warm and wet climate (Kalaitzidis et al., 2004).

3. Material and methods

The material described in the present paper is composed of 395 fossil remains of amphibians and reptiles. The material is permanently curated in the collections of the University of Utrecht, The Netherlands. All the pictures presented herein were taken with a Leica M205 microscope at the Department of Earth Sciences, University of Turin, Italy. Specimens were photographed using the software Leica Application Suite V4.10 with the exception of the indeterminate Scinciformata/Laterata (UU NO1 1016 and UUNO1 1038) and Scincidae (UU NO1 1036) specimens, which were photographed with a Jeol JSM-IT300LV Scanning Electron Microscope in the same institution. All measurements were made with a caliper.

The anatomical terminology used here in the description of the amphibians follows mainly the one of Bailon (1999) and Rage (1974). Additional terminology used to describe the specimens of *Latonia* comes from Roček (1994). As for the reptiles, the terminology used follows Hervet (2000) for turtles, Szyndlar (1984) and Hoffstetter and Gasc (1969) for snakes. For the non-ophidian squamates (i.e., “lizards”), it follows Hoffstetter and Gasc (1969) for the vertebral elements and Barahona and Barbadillo (1997) for the cranial elements. The terminology used to describe tooth structures for the dentary UU NO1 1016 is that of Richter (1994).

Taxonomy follows Pyron and Wiens (2011) for the amphibians, Crawford et al. (2015) for the turtles, Gauthier et al. (2012) and Zheng and Wiens (2016) for the squamates.

In the following section, the localities cited in the material list are chronologically arranged.

Institutional abbreviations: MDHC, Massimo Delfino Herpetological Collection, Department of Earth Sciences, University of Turin, Turin, Italy; UU, Department of Earth Sciences, University of Utrecht, Utrecht, The Netherlands.

4. Systematic palaeontology

Amphibia Linnaeus, 1758

Anura Fischer von Waldheim, 1813

Alytidae Fitzinger, 1843

Latonia von Meyer, 1843

***Latonia* sp.**

Figs. 2–4

Material: TE1: three left maxillae (UU TE1 1501 [two specimens] and UU TE1 1525); one right maxilla (UU TE1 1502); two fragments of frontoparietal (UU TE1 1512 and UU TE1 1533); four left angulars (UU TE1 1504, UU TE1 1506 and UU TE1 1526 [two specimens]); two right angulars (UU TE1 1503 and UU TE1 1505); three trunk vertebrae (UU TE1 1511); one left humerus (UU TE1 1507); one left radioulna (UU TE1 1510); two left ilia (UU TE1 1508 and UU TE1 1509); one right ilium (UU TE1 1527). TE2: one right maxilla (UU TE2 1520); one left maxilla (UU TE2 1521); one frontoparietal (UU TE2 1506); two trunk vertebrae (UU TE2 1507); one urostyle (UU TE2 1518); one left ilium (UU TE2 1522). KO1lowB: one left humerus (UU KO1lowB 1502); one radioulna (UU KO1lowB 1501). KO1highA: one left humerus (UU KO1highA 1501); one right ilium (UU KO1highA 1502). VOR1: one left ilium (UU VOR1 1503). TE3: one right maxilla (UU TE3 1525); three right angulars (UU TE3 1504, UU TE3 1506 and UU TE3 1522); two left angulars (UU TE3 1505 and UU TE3 1521); one trunk vertebra (UU TE3 1502); one left scapula (UU TE3 1526); one coracoid (UU TE3 1527); two right ilia (UU TE3 1503 and UU TE3 1524); one left ilium (UU TE3 1523); one tarsal (UU TE3 1529). VOR2: one left maxilla (UU VOR2 1503); one right maxilla (UU VOR2 1504); one right angular (UU VOR2 1502); one urostyle (UU VOR2 1505); one radioulna (UU VOR2 1507); one left ilium (UU VOR2 1506). VOR3: two right maxillae (UU VOR3 1503 and UU VOR3 1524); one left angular (UU VOR3 1504); one right angular (UU VOR3 1505); three urostyles (UU VOR3 1501, UU VOR3 1530, and UU VOR3 1531); one left ilium (UU VOR3 1502); one atlas (UU VOR3 1506); two sacral vertebrae (UU VOR3 1507); one radioulna (UU VOR3 1532). VOR3A: two right maxillae (UU VOR3A 1517 [two specimens]); one frontoparietal (UU VOR3A 1518); two left angulars (UU VOR3A 1516 and UU VOR3A 1527); one atlas (UU VOR3A 1521); one trunk vertebra (UU VOR3A 1524); two heavily fragmented trunk vertebrae (UU VOR3 1525); two sacral vertebrae (UU VOR3A 1522 and UU VOR3A 1523); one urostyle (UU VOR3A 1511); two right humeri (UU VOR3A 1519); two radioulnae (UU VOR3A 1520); one tibiofibula (UU VOR3A 1526). VOR4: two left maxillae (UU VOR4 1503); one right maxilla (UU VOR4 1504); one left angular (UU VOR4 1507); two atlases (UU VOR4 1508); one sacral vertebra (UU VOR4 1509); one left humerus (UU VOR4 1510); one radioulna (UU VOR4 1505); one tibiofibula (UU VOR4 1506). VOR8: one left maxilla (UU VOR8 1502); one trunk vertebra (UU VOR8 1504); one right humerus (UU VOR8 1503). NO1: two left maxillae (UU NO1 1005 and UU NO1 1058); one right maxilla (UU NO1 1059); two right angulars (UU NO1 1009 and UU NO1 1057); three left angulars (UU NO1 1008 [two specimens] and UU NO1 1056); one scapula (UU NO1 1060); two left humeri (UU NO1 1054); two right humeri (UU NO1 1006 and UU NO1 1055); two radioulnae (UU NO1 1007 and UU NO1 1061); one right ilium (UU NO1 1050).

Description: Angular: These specimens reach a relatively very large size, ranging from around 4 mm long to 17 mm long. The bones are on average well preserved, but some of them miss their anterior portion (Fig. 2A–B). They are S-shaped and display both a coronoid and a paracoronoid process. The coronoid process shows small variation among all the specimens in the degree of elongation. Moreover, it slightly extends posteriorly in UU TE1 1506 and UU VOR2 1502, whereas there is no sign of posterior extension in all the other specimens in which the preservation of this process is good enough. The sulcus pro cartilago Meckeli is quite deep and deepens and widens in its posterior part.

Maxillae: This material shows a different degree of preservation, with specimens that are either very fragmentary or more preserved (although never complete; Fig. 2C–H). Size also varies, including both smaller fragments and rather large specimens, with the largest one reaching a length of 14.7 mm. These elements show a depression on the medial surface posterior to the pterygoid process. The lamina horizontalis is relatively thin given the general size of the bones. At least some of the maxillae preserve a lateral surface that is not perfectly smooth, displaying clear rugosities that increase in development in the largest specimens (UU TE1 1501 and UU VOR4 1503). Other specimens, on the other hand, are laterally smooth. When the posterior end is preserved, the tooth row extends posteriorly to the moderately thin lamina horizontalis. The pterygoid process is present, even though never completely preserved.

Frontoparietal: These specimens are fragmentary (Fig. 2I–L). UU TE1 1512 and UU TE1 1533 consist in separate portions of what seems to be the anterior part of a single frontoparietal (Fig. 2I–J). Tubercles displayed in a parallel to sub-parallel orientation are present on the dorsal surface of the bone. In ventral view, a strong longitudinal ridge is present. This structure is interpreted as the pars contacta of the bone. UU TE2 1506 and UU

VOR3A 1518 are smaller fragments, which display a dense network of small tubercles connected by numerous low and deep ridges.

Atlases: All the atlases are only represented by their centrum (Fig. 3A–H). UU VOR3 1506 is slightly larger than the others with a 4.8 mm long centrum compared to the 3.3 mm long centrum in both specimens from Vorio 4 and the 3.5 mm long centrum of the specimen from Vorio 3A. On their ventral surface, all atlases are provided with a strong crista ventralis, which is almost as long as the centrum itself (slightly shorter in UU VOR3A 1521; Fig. 3B and 3F). On the posterior end of the ventral surface of the centrum, there is a pronounced depression (shallower in UU VOR3A 1521) on both sides of the crista ventralis. The cotyles on the anterior end of the centrum are well defined and separated (a cotylaric type II of Lynch (1969) = anterior cotyles close but not confluents). Posteriorly, a subcircular cotyle is present.

Trunk vertebrae: These vertebrae are poorly preserved and most of the structures are damaged (Fig. 3I–L). Their length ranges from 2.5 mm long to 6.5 mm. They are opisthocoelous, with a very slightly dorsoventrally compressed centrum that seems to be circular to subcircular in section. When preserved, the neural canal is oval. Their ventral surfaces are smooth.

Sacral vertebrae: The Vorio 3 specimens and one of those from Vorio 3A (UU VOR3A 1522) are not well preserved, showing only their ventral portion, whereas the Vorio 4 specimen (UU VOR4 1509) and UU VOR3A 1523 are in better preservation state but still damaged (Fig. 3M–P). These vertebrae are identified as sacrals on the basis of the presence of an anterior condyle and two condyles on the posterior part of the centrum and the morphology of the sacral processes (just for UU VOR4 1509 and UU VOR3A 1523 in the latter case). These processes, though partially broken, are not perpendicular to the body axis but rather directed posterolaterally.

Urostyles: UU VOR3 1501 is well preserved, whereas the degree of preservation is lower in the other specimens (Fig. 3Q–V). UU VOR3 1501 is 22.1 mm long and displays a thin dorsal fissure running along its neural crest. The cotyles on this urostyle are oval, well defined and distinct from each other, although the left condyle is slightly eroded. The intervertebral canals are present, as well as transverse processes by the anterior end of the neural arch. The morphology of the other urostyles is comparable, at least as far as their preserved portions are concerned.

Scapula: In the two specimens, the preservation state is poor. Indeed, only portions of the pars suprascapularis of these skeletal elements are partially preserved. The pars glenoidalis and pars acromialis are broken (Fig. 4A–B). In the anterior margin, a well-developed tenuitas cranialis is visible. The scapula does not seem to have been much elongated.

Coracoid: The preserved portion of this element is straight, but the pars epicoracoidealis is broken off (Fig. 4C). The intumescentia glenoidalis is subcircular and lightly compressed dorsoventrally. The diameter of the latter structure is 4 mm, whereas the diameter is only 2 mm in the portion preceding the pars epicoracoidealis.

Humeri: The available humeri are fragmentary, preserving only a small part of the diaphysis and part of the distal end to some extent (Fig. 4D–I). They are large-sized with the largest specimen (UU TE1 1507) being 9 mm long, 9 mm wide and provided with a 6 mm wide humeral ball. The distal end has an asymmetrical appearance, with the humeral ball shifted towards the lateral side. When preserved, the epicondylus ulnaris is more developed and robust than the epicondylus radialis. These fragments also display a large and robust crista medialis. The crista lateralis is present but smaller than the crista medialis. The fossa cubitalis ventralis is either light and shallow or not clearly visible on these humeri.

Ilia: Except for the smaller UU VOR1 1503 and UU TE3 1523, this material is composed of large-sized ilia (Fig. 4J–M). Few specimens display the anterior branch and dorsal margin, with the Vorio 3 specimen being the best preserved. This specimen is 20.7 mm long. The concavity of the dorsal crest is also pronounced. The dorsal crest is medially curved. The fossula tuberis superioris is pierced by one or more foramina. The preservation is generally poor enough as the acetabula are absent and both pars ascendens and pars descendens are broken. Only UU TE1 1509 preserves the posterior end of the ilium. It displays a moderately long pars ascendens, a well-developed pars descendens, and a subtriangular acetabulum. On its medial surface, an interiliac groove and an interiliac tubercle are visible.

Radioulna, tibiofibula, tarsus: Given that these three types of skeletal elements do not bear any morphological structure with much taxonomic implication, they are not of any help to the identification. They will not be described here, except for a general robustness and large size, which matches the general morphology of these bones in *Latonia* (Fig. 4N).

Remarks and comparisons: All these elements agree in terms of both size and morphology with discoglossine alytid frogs of the genus *Latonia*. A combination of features useful to support this assignment is the following (Roček, 1994, 2013; Biton et al., 2013, 2016): presence of a posterior depression on the maxilla; presence of both coronoid and paracoronoid processes; sulcus pro cartilago Meckeli that deepens posteriorly; ventrally located median keel on the atlas; laterally-shifted humeral ball. *Latonia* species identification is complicated by the fact that taxa of this genus have been described either based on articulated specimens on slabs or on isolated, disarticulated bones. An overview of some useful characters was recently provided by Syromyatnikova and Roček (2018), though. We here discuss those that are significant for the identification of our fossils.

One of the main features that was used in the past to discriminate between different species of *Latonia* was the presence/absence of dermal sculpturing on the maxilla. A sculptured maxilla was for a long time considered typical for *Latonia gigantea* (Lartet, 1851) (which some recent evidences suggested that this taxa is actually a junior synonym of *Latonia seyfriedi* Meyer, 1843 (Syromyatnikova et al., 2019)), in contrast with *Latonia ragei* Hossini, 1993 and *Latonia vertaizoni* (Friant, 1944) (Roček, 1994, 2013; Syromyatnikova and Roček, 2018). A smooth maxilla was recently reported also in *Latonia nigriventer* (Mendelssohn and Steinitz, 1943) (Biton et al., 2016) and *Latonia caucasica* (Syromyatnikova and Roček, 2018). Most of the maxillae from the Ptolemais Basin look unsculptured, but this is most likely due to the fact that they either represent fragments of the middle or anterior portion of the bone or smaller, younger individuals. Nevertheless, a poorly developed ornamentation (mostly rugosities) is present in at least some specimens. This appears somehow similar to the one present on maxillae from the early Miocene of Karydia 3 assigned to *Latonia* cf. *gigantea* (now *Latonia* cf. *seyfriedi*) (Georgalis et al., 2019a), though those are clearly smaller than the one described here.

Ornamentation on the frontoparietal also has some taxonomical significance (Roček, 1994, 2013; Biton et al., 2016; Syromyatnikova and Roček, 2018): an unsculptured frontoparietal is present in *L. nigriventer*, *L. ragei*, *L. caucasica*, and the Ptolemais material, but not in *L. seyfriedi*. The Ptolemais maxillae display a tooth row that extends posteriorly beyond the pterygoid process, like *L. seyfriedi* (*L. gigantea* included), *L. ragei*, and *L. nigriventer* and unlike *L. caucasica* (Biton et al., 2016; Syromyatnikova and Roček, 2018). The posterolaterally directed sacral transverse processes are found in *L. seyfriedi* (*L. gigantea* included) and *L. ragei*, but not in the other *Latonia* species (Roček, 1994, 2013; Biton et al., 2013, 2016; Syromyatnikova and Roček, 2018; Syromyatnikova et al., 2019). Moreover, the Ptolemais humeri recall *L. seyfriedi* (*L. gigantea* included) in having a fossa cubitalis ventralis that is either absent or shallow (Syromyatnikova and Roček, 2018). The fossa is shallow in *L. caucasica* too, but deeper in *L. ragei*.

Combined, all these features seem to point towards affinities with *L. seyfriedi* (*L. gigantea* included) for the Ptolemais *Latonia* material as a whole. However, this attribution is complicated by the morphology of the coronoid process of the angulars. As a matter of fact, Syromyatnikova and Roček (2018) reported the presence of a posteriorly extended coronoid process only in *L. ragei*. The unextended process is on the other hand present in all other species and rarely also in *L. ragei*. The presence of both morphologies in the herein described material is therefore puzzling and the possibilities of two different taxa represented cannot be excluded a priori, even though the few material that could suggest this (only two angulars) might render it unlikely. Nevertheless, the extended coronoid process cannot be used as a clear diagnostic feature of *L. ragei* either, as it is also present in still unpublished *Latonia* material from the Pleistocene of Italy that most likely do not pertain to such species (Sorbelli, pers. comm. to AV, May 2019). Thus, the Ptolemais *Latonia* is here only identified at genus level, pending a thorough revision of the diagnostic features of the different species.

Ranidae Rafinesque, 1814

Rana Linnaeus, 1758

***Rana* sp.**

Fig. 5A–J

Material*:* TE2: one left ilium (UU TE2 1501). TE3: two right humeri (UU TE3 1501 and UU TE3 1532); three left ilia (UU TE3 1530); one left humerus (UU TE3 1531). VOR3A: two right humeri (UU VOR3A 1509); one right ilium (UU VOR3A 1510). NO1: one left humerus (UU NO1 1003); two right ilia (UU NO1 1004 and UU NO1 1025); one left ilium (UU NO1 1049).

Description: Humeri: The preservation of these specimens is variable; however, they all present at least the distal end of the bone (Fig. 5A–F). In some, the humeral ball is highly eroded or even absent. Due to their poor preservation, the surviving portion of UU TE3 1531 and UU TE3 1532 is relatively small. The length of the better-preserved humeri is around 7 mm and even reaches 8.6 mm in UU TE3 1501, which is relatively well preserved. In ventral view, the diaphysis is straight. The humeral ball is not laterally shifted but rather positioned right in the extension of the main axis of the bone. A shallow fossa cubitalis ventralis is displayed on these humeri and this structure is closed both laterally and medially. None of the remains displays a crista paraventralis. The best-preserved specimens, presenting a more complete diaphysis, show a well-developed medial crest that slightly bends towards the dorsal side.

Ilia: These eight ilia are of various sizes and relatively damaged (Fig. 5G–J). The smallest specimen (UU NO1 1004) is 3 mm long and only displays a portion of the acetabulum and base of the anterior branch. The largest specimen (UU TE2 1501) is 10 mm long and the preserved structure consists in a portion of the dorsal crest, the acetabulum and a portion of the anterior branch. The dorsal crest, although rarely well-preserved shows moderate to high elevation and is straight. The preserved portion of these ilia is not pierced by any foramen. In medial view, they are deprived of interiliac tubercle and groove. These specimens display a large and slightly convex tuber superior. This structure is especially visible on UU TE2 1501. The pars ascendens and pars descendens are broken in all specimens. Nevertheless, the dorsal margin of the well-defined tuber of UU TE2 1501 appears rather low, suggesting that the angle formed by it and the pars ascendens was rather wide.

Remarks: The material here described is assigned to *Rana* sp. on the basis of the following features of the humeri: the spherical humeral ball, a straight diaphysis, a shallow fossa cubitalis ventralis and a well-developed medial crest (Bailon, 1999). The latter is dorsally curved (Fig. 5B), which is a feature of male brown frogs (*Rana* sensu stricto) whereas this structure is short and transversally extended in males individuals of *Pelophylax* Fitzinger, 1843 (Torres-Roig et al., 2017). The herein described ilia look similar to the ilia of

Latonia of the Ptolemais material described above, but they can be distinguished from *Latonia* by the absence of interiliac groove, interiliac tubercle and the absence of foramina on the fossula tuberis superioris, which are common in latter genus (Roček, 1994; Syromyatnikova and Roček, 2018). These ilia are similar to what is known in *Rana* sensu stricto, but their preservation makes the observation of specific diagnostic features difficult, thus hindering a more precise identification for this material. The convexity of the tuber superior allows discriminating these ilia from those of *Pelophylax* as this structure is flattened laterally in the latter genus (Ratnikov, 2001; Colombero et al., 2014; Blain et al., 2015; Syromyatnikova, 2016).

Ranidae indet.

Fig. 5K–V

Material: TE1: one right angular (UU TE1 1530). VOR1: one left maxilla (UU VOR1 1502). TE3: one left humerus (UU TE3 1509); two right humeri (UU TE3 1510); one left radioulna (UU TE3 1512). VOR2: one right humerus (UU VOR2 1512); one left angular (UU VOR2 1513). VOR3A: one left maxilla (UU VOR3A 1514); one right maxilla (UU VOR3A 1515). VOR4: one right angular (UU VOR4 1502). NO1: two urostyles (UU NO1 1023 and UU NO1 1047); one left humerus (UU NO1 1051); two right humeri (UU NO1 1052).

Description: Angular: The smallest angular (UU VOR4 1502) is 8.5 mm long and the largest one (UU VOR2 1513) is 11.8 mm long. They display a single coronoid process which is high, well developed, almost vertical and do not extend strongly neither anteriorly nor posteriorly (Fig. 5K–O). The crista paracoronoidea is vertical (Fig. 5L and 5N). Between this crest and the coronoid process, there is a shallow depression. The sulcus pro cartilago Meckeli is deep and has a moderate S-shape.

Maxillae: These elements are small-sized and slightly elongated (Fig. 5P–R); the smallest fragment is 4.5 mm long and the largest one is 8.5 mm long. All specimens preserve only the middle portion of the bone: the posterior and anterior ends are broken. They are provided with pedicellated teeth. The lamina horizontalis is thick and slightly convex in dorsal view. The labial surface of the maxilla is smooth.

Urostyles: They are broken in the posterior part and small-sized. Both of them are 4.3 mm long. They do not show any lateral apophysis. The sacro-urostylar articulation is bicondylar. The cotyles are subcircular and well defined. They both show a broken but high dorsal crest and narrow neural canal.

Humeri: These elements are small-sized, slender and relatively poorly preserved. The humeral ball is eroded in UU TE3 1509. These humeri appear not to have a crista medialis. In ventral view, the diaphysis is straight and the humeral ball is not shifted. The humeral ball is spherical. A shallow and closed fossa cubitalis ventralis is also present.

Remarks*:* The material here described display features, such as the absence of palatal process and elongation of the maxilla and a straight diaphysis, a spherical humeral ball and a shallow fossa cubitalis ventralis for the humerus, that are characteristic of both brown frogs and green frogs according to Bailon (1999). Radioulnae usually do not bear diagnostic features, however, this one is only moderately elongated (Fig. 5S–V), which recalls the morphology in Ranidae. The humerus is an element that can be used to discriminate between *Rana* sensu stricto and *Pelophylax* by looking at the robustness of the diaphysis and the morphology of the crista medialis (Bailon, 1999; Torres-Roig et al., 2017). However, this only applies to adult male individuals and the humeri here described are slender and do not display a crista medialis. They likely belonged to juvenile and/or female individuals. Hence, the distinction between the two taxa cannot be made here and these specimens are identified as Ranidae indet.

(non-Bufonidae) Anura indet.

Fig. 6A–C

Material: TE1: three right maxillae (UU TE1 1517 and UU TE1 1528 [two]). TE3: eight right maxillae (UU TE3 1507 [two], UU TE3 1508, UU TE3 1537 [three] and UU TE3 1539 [two]); four left maxillae (UU TE3 1538). VOR3: three right maxillae (UU VOR3 1514 and UU VOR3 1515 [two]). VOR3A: one left maxilla (UU VOR3A 1502); four right maxillae (UU VOR3A 1513). VOR4: one right maxilla (UU VOR4 1501). NO1: one right maxilla (UU NO1 1018); two left maxillae (UU NO1 1017 and UU NO1 1046).

Description: The material listed above consist of numerous (27) maxillae. Their average preservation is quite poor; however, it ranges from heavily fragmented remains to moderately fragmented remains. The length of the preserved portions is variable, ranging from 2.3 mm for the shortest specimen (UU NO1 1046) to 9.1 mm for the largest one (UU TE1 1517). Among all of these remains, several morphologies can be observed, especially on the lamina horizontalis, which is either quite thin or relatively thick, and on the teeth orientation (e.g., some have a straight implantation, whereas others have their implantation directed slightly frontward or backward). The only feature common to every one of those specimens is the presence of teeth (Fig. 6A).

Remarks: Due to the high variability in the preservation status of this material and therefore the lack of diagnostic features, it is not possible to identify confidently each specimen further than at order level. However, the presence of teeth is a clear argument in favor of the exclusion of the Bufonidae family from the list of all the taxa these fossils could belong to (Bailon, 1999). Nonetheless, the morphological differences pointed out earlier strongly suggest that the material is composed of several taxa, such as the already identified

Ranidae or *Latonia* (especially when considering specimen UU TE1 1517, the size of which could be coherent with the latter; Roček, 1994).

Anura indet.

Fig. 6D–L

Material: TE1: one sacral vertebra (UU TE1 1519); three urostyles (UU TE1 1518 and UU TE1 1532 [two]); one radioulna (UU TE1 1524); two distal phalanges (UU TE1 1521); two left ilia (UU TE1 1529 and UU TE1 1531); one femur (UU TE1 1522); 13 tarsals (UU TE1 1520 [12] and UU TE1 1523). TE2: one trunk vertebra (UU TE2 1525); two sacral vertebrae (UU TE2 1524 and UU TE2 1526); two urostyles (UU TE2 1519); two radioulnae (UU TE2 1528); two right ilia (UU TE2 1523); two tarsals (UU TE2 1527). TE3: one right angular (UU TE3 1535); two vertebrae (UU TE3 1528 and UU TE3 1542); three urostyles (UU TE3 1511 [two] and UU TE3 1534); 13 radioulnae (UU TE3 1513[three] and UU TE3 1540 [10]); one left ilium (UU TE3 1536); four tarsals (UU TE3 1514 [two], UU TE3 1515 and UU TE3 1517); 14 undetermined fragments (UU TE3 1516 [eight] and UU TE3 1541 [six]); one distal phalanx (UU TE31533). VOR2: two urostyles (UU VOR2 1511 and UU VOR2 1517); one tarsal (UU VOR21508); one distal phalanx (UU VOR2 1510). VOR3: one squamosal (UU VOR3 1522); two urostyles (UU VOR3 1518 and UU VOR3 1519); two femurs (UU VOR3 1517 and UU VOR3 1529); three tarsals (UU VOR3 1527 [two] and UU VOR3 1528); one distal phalanx (UU VOR3 1516). VOR3A: one left angular (UU VOR3A 1512); two tarsals (UU VOR3A 1501 and UU VOR3A 1503). NO1: one vertebra? (UU NO1 1020); one sacral vertebra (UU NO1 1045); two urostyles (UU NO1 1024 and UU NO1 1048); one left ilium (UU NO1 1019); two tarsals (UU NO1 1021); two distal phalanges (UU NO1 1053); one undetermined fragment (UU NO1 1022).

Remarks: The material listed above is quite diversified in the variety of skeletal elements (Fig. 6D–L). However, the majority of these specimens are much fragmentary and/or do not bear any clear diagnostic features that would allow any tentative identification further than Anura. Numerous isolated pieces of appendicular skeleton (e.g. tarsals, phalanges) have been found, but based on our current knowledge, they do not possess any known diagnostic features and thus they are of no use in the identification process. It is very likely that there are several distinct taxa represented in this material but this cannot be confirmed at the moment. At least some of the specimens could pertain to the above described *Latonia* due to their very large size, but their belonging to another, large-sized anuran cannot be totally discounted mainly due to their fragmentary nature. The presence in the Ptolemais Basin of a third anuran taxon might be suggested by the sacral vertebra UU TE1 1519, the morphology of which is not compatible with either *Latonia* or Ranidae. This vertebra preserves only the centrum, which is strongly dorsoventrally compressed. The anterior condyle is very wide and elliptical. Posteriorly, it has two small and subcircular condyles, which are distinctly separated from one another.

Reptilia Laurenti, 1768

Testudines Batsch, 1788

Cryptodira Cope, 1868

Testudinoidea Fitzinger, 1826

Testudinidae Batsch, 1788

Testudo Linnaeus, 1758

cf. *Testudo* sp.

Fig. 7

Material: NO1: one peripheral (UU NO1 1071 [two fragments]).

Description: This incomplete peripheral is separated in two portions, rather large-sized, reaching a total length of 35 mm (Fig. 7A–B). It is provided with a very fine vermiculated ornamentation on the external surface. It is medio-laterally thick, vertically-oriented and the free edge displays a cutting edge (Fig. 7C). The scar of the inguinal buttress appears to be confined to this shell element, very close to its anterior edge. On its inner surface, there is a small, elongated inguinal shield. A longitudinal scute sulcus runs on the external surface and can be followed on the inner surface.

Remarks: This specimen is interpreted as representing the seventh left peripheral located on the posterior opening of the shell and therefore partially involved in the bridge (alternatively, it could be the eighth peripheral, but this seems less likely). The absence in UU NO1 1071 of a pleuro-marginal sulcus, and therefore the presence of a single sulcus on the external surface, can be interpreted as the coincidence of the costo-peripheral suture with the pleuro-marginal sulcus. This particular feature is reminiscent of *Testudo* sensu lato (*Chersine* Merrem 1820 and *Agrionemys* Khosatzky and Młynarski 1966 included) (Hervet, 2000; Vlachos et al., 2015, and references therein). The seventh peripheral in extant specimens of *Testudo graeca* Linnaeus, 1758 (MDHC 220), *Testudo hermanni* Gmelin, 1789 (MDHC 379) and *Testudo marginata* Schoepff, 1792 (MDHC 370) clearly differs in morphology from UU NO1 1071. In the fossil specimen, the inferred bridge morphology seems to indicate that the bridge is shorter than in these three taxa where the inguinal buttress develops in the posterior area of the seventh peripheral of even reaches the eight one. However, quantitative analyses of this character among *Testudo* are lacking, thus hindering the appreciation of its possible variability. Because of this and, above all, because of its fragmentary nature and poor representativeness, UU NO1 1071 is here tentatively identified as cf. *Testudo* sp.

Testudinoidea indet.

Fig. 8

Material: VOR1: one costal fragment (UU VOR1 1507); two indeterminate shell fragments (UU VOR1 1506). TE3: one neural fragment (UU TE3 1543); one indeterminate shell fragment (UU TE3 1518). VOR2: three costal fragments (UU VOR2 1501, UU VOR2 1520-1521). VOR3: one distal phalanx (UU VOR3 1526). VOR3A: one neural plate fragment (UU VOR3A 1504). NO1: two costal fragments (UU NO1 1001 and UU NO1 1073); one shell fragment (UU NO1 1074).

Description: This material consists of several small and isolated fragments of chelonian shells and one distal phalanx. It is worth noting that in some cases (e.g., UU NO1 1070 and UU NO1 1074) several fragments are in fact parts of a unique plate. The elements described here are provided with a very fine vermiculated ornamentation on their external surface, whereas their inner surface seems generally smooth. There is no developed sculpturing or high ornamentation in any specimen. Some elements host a scute sulcus on their external surface.

The specimens from Vorio 1 are small rectangular fragments (Fig. 8A–B). The vermiculated ornamentation is less pronounced on the costal UU VOR1 1507 than on any other specimen.

Both Tomea Eksi 3 specimens are small-sized. UU TE3 1518 does not allow to confidently place it on a shell, whereas UU TE3 1543 is a fragment of a rectangular neural (Fig. 7B–C).

UU VOR2 1501 is 22 mm long and 14.8 mm wide. It is roughly rectangular and displays several tight growth sulci on its external surface (Fig. 8E–G). A longitudinal sulcus that is not associated with the vertebral and pleural sulci is present. This element displays a broken costal process. UU VOR2 1520 is a fragment of a costal plate. It is 8 mm long. On its visceral surface, it displays a rib. Although being fragmented, UU VOR2 1521 is here interpreted as a fragment of a costal plate on the basis of what seems to be a broken costal process.

The incomplete neural UU VOR3A 1504 is slightly hexagonal in shape, longer than wide characterized by a straight, robust and convex ridge placed sagittaly on its inner side (Fig. 8H–J). On the external surface, a narrow and shallow sulcus runs perpendicularly to the previously-described ridge.

The shape of the fragments from Notio 1 appears to be rather more trapezoidal than rectangular. UU NO1 1001 is the distal portion of a costal (Fig. 8K–M), which stands out from the other specimens by its larger size. Its main length reaches 19.6 mm. It has an external surface provided with a marked scute sulcus. Perpendicular to this sulcus and also on the external surface of the specimen, the presence of smaller and tight growth sulci can be noted. In cross section, the external surface is slightly concave and the posterior end of the external surface slightly bent ventrally. The costal UU NO1 1073 is 10 mm long (Fig. 8N–P). Its external surface hosts a fine vermiculated ornamentation, whereas the smooth visceral surface displays a sort of longitudinal ornamentation represented by elongated grooves. The visceral surface of this element is provided with rib. UU NO1 1074 is small-sized (the main length being 12 mm long), fragmentary and lacks any structures that could enable a more precise identification within the shell.

The phalanx UU VOR3 1526 is large, reaching 15.8 mm long (Fig. 8Q). It is slightly hooked and the ventral surface is relatively flat.

Remarks: The above-described material clearly pertains to Testudines but it is too much fragmentary to allow a more precise taxonomic identification. However, the overall morphology is reminiscent of testudinoids. Such assumption is further supported by the fact that pleurodires are only known from the early Miocene of the area (Georgalis et al., 2013; Georgalis and Kear, 2013), chelydrids are totally absent (Georgalis and Kear, 2013), whereas trionychids that are present in the late Miocene and Pliocene of Greece have a drastically different morphology also because they possess a characteristic sculpturing pattern (Georgalis and Joyce, 2017). It is also worth noting that UU VOR2 1501 displays an unusual morphology in showing growth marks parallel to a longitudinal sulcus rather than perpendicular to it.

Squamata Oppel, 1811

Scinciformata Vidal and Hedges, 2005

Scincidae Gray, 1825 (*sensu* Hedges, 2014)

Scincidae indet.

Fig. 9

Material: NO1: one right dentary (UU NO1 1036).

Description: The sole known specimen, the right dentary UU NO1 1036 is fragmentary, missing both its two ends. It is 4.3 mm long. The posterior part of the Meckelian fossa is medially opened, whereas in its anterior part, the fossa is enclosed in a rather narrow and tubular structure (Fig. 9B). This structure originates from a ventral expansion of the slender subdental shelf (sensu Rage and Augé, 2010). Three teeth out of the 17 tooth positions present are preserved, even though the crown is completely preserved only in two of them. Teeth are pleurodont, cylindrical and slender; when preserved, their crown is dorsally rounded and show both a labial and a lingual longitudinal cusp. The crown is also slightly, but distinctly enlarged anteroposteriorly. On the lingual side of the crown, light striae are visible

(Fig. 9C). The lateral surface of the dentary is smooth, except for the presence of a single mental foramen.

Remarks: The morphology of the teeth present on this specimen recalls the common dentition observed in Scincidae in having crowns provided with two longitudinal cusps and a light lingual striation (Townsend et al., 1999; Villa and Delfino, 2019). The identification of this specimen as a scincid is also supported by the partial closing of the Meckelian fossa due to ventral expansion of the subdental shelf, which can be seen sometimes on dentaries of this clade (Caputo, 2004; Villa and Delfino, 2019). Certain features of UU NO1 1036 enable us to differentiate it from all three extant scincids that occur in the Greek mainland (Camaiti et al.,2019; Villa and Delfino, 2019): the partial closing of the Meckelian fossa due to ventral expansion of the subdental shelf allows our specimen to be distinguished from the extant *Ablepharus kitaibelii* Bibron and Bory de Saint-Vincent 1833 (which has an almost entirely closed Meckelian fossa), whereas the slender teeth differentiate it from both *Chalcides ocellatus* Forskål 1775 and *Ophiomorus punctatissimus* Bibron & Bory de Saint-Vincent 1833. The slight anteroposterior enlargement of the preserved teeth of this specimen also distinguish it from other extant European species of *Chalcides* Laurenti, 1768 and from *Heremites auratus* (Linnaeus, 1758) (referred as *Trachylepis aurata;* Villa & Delfino, 2019).

Laterata Vidal and Hedges, 2005

Lacertidae Gray, 1825

Lacertidae indet.

Fig. 10A–F

Material: TE1: one premaxilla (UU TE1 1515). TE2: one fragmented tooth bearing bone (UU TE2 1504). NO1: one left dentary (UU NO1 1037).

Description: Premaxilla: This specimen is small-sized and incomplete (Fig. 10D–F). Only most of the nasal process and the left part of the premaxillary shelf (which is 1.9 mm long) is present. The ascending nasal process has subparallel lateral margins and its external surface is ornamented. This premaxilla preserves three pleurodont, cylindrical and slender teeth, none of which preserves the crown.

Dentary: This specimen is 6.4 mm long (Fig. 10A–C). Its anterior and middle portions are preserved. Eight teeth are preserved, displaying a pleurodont, cylindrical and slender morphology. All of the preserved teeth are bicuspid with a main cusp provided with a smaller lateral cusp on anterior position. The Meckelian fossa is quite long, wide and medially opened and it is steadily narrowing toward the anterior end of the dentary. It also displays curved dorsal and ventral margins. A narrow subdental shelf (sensu Rage and Augé, 2010) is present on the specimen, hosting a subdental ridge and a sulcus dentalis dorsally.

Tooth-bearing bone: Specimen UU TE2 1504 is in such an extreme degradation state that it cannot be confidently identified. The teeth it bears are cylindrical, pleurodont and relatively robust. Their crowns are not well preserved. Due to its extreme fragility, the specimen was damaged during manipulation and it is now even more fragmented. However, tooth morphology is still recognizable.

Remarks: Aside from the fact that the Tomea Eksi 2 tooth bearing bone is so poorly preserved that its lacertid nature can be recognized only based on tooth morphology, the morphology of the other elements (the subparallel margins of the nasal process of the premaxilla (a common feature in lacertids lizards), the fully opened Meckelian fossa, the curvature of its dorsal and ventral margins and the pleurodont and cylindrical tooth morphology, which is bicuspid [Morphotype G as defined by Kosma (2004)] in the dentary) taken together allows referral of these specimens to Lacertidae (Barahona and Barbadillo, 1997; Augé, 2005; Augé and Hervet, 2009; Blain et al., 2013; Čerňanský and Augé, 2013; Georgalis et al., 2017; Sen et al., 2017; Villa and Delfino, 2019).

Scinciformata or Laterata indet.

Figs. 10G–K, 11

Material: TE2: one anterior caudal vertebra (UU TE2 1502); three trunk vertebrae (UU TE2 1503). NO1: one right dentary (UU NO1 1016); one left dentary (UU NO1 1038).

Description: Dentaries: Both these dentaries are highly fragmentary (Fig. 11). They display pleurodont, cylindrical and slender teeth. In UU NO1 1038, none of the crowns is preserved, thus preventing to recognize a clear morphology. On the other hand, these are preserved in at least two of the three teeth still present on UU NO1 1016, which are the three most anterior dentary teeth. The crowns of teeth of UU NO1 1016 are flattened lingually and display two facets that are respectively distinctly facing anterolingually and posterolingually (Fig 11A–B). These facets are delimited lingually by low striae dominantes and labially by well-developed cristae mesialis and distalis. A lingual cusp, formed by the meeting of striae and both cristae mesialis and distalis is present. The labial surfaces of the teeth are convex. The labial cusp is distinctly bent lingually. Both lingual and labial cusp are connected by a distinct carina intercuspidalis. Anguli mesialis and distalis are distinct, but strongly rounded. Both the labial and the lingual sides of the tooth crowns of UU NO1 1016 are not distinctly striated (only very light striae might be present). In both dentaries, a sulcus dentalis, flanked by a subdental ridge, is visible on the subdental table (*sensu* Rage and Augé, 2010) along the tooth row. UU NO1 1016 also shows a narrow and subhorizontal mandibular symphysis.

Trunk vertebrae: These are rather fragmentary and their centrum size ranges between 2 and 3.2 mm in length. Only one of them has its neural arch still present, but it is too poorly preserved to display significant morphological features.

Caudal vertebra: The specimen is relatively large with a subcircular to slightly oval centrum, reaching a total length of 2.9 mm (Fig. 10G–K). The left transverse process is partially broken. The neural arch displays a short neural spine. The ventral surface of this vertebra does not seem to present a keel.

Remarks: Due to their fragmentary nature, it is not possible to provide a more precise identification of the specimens to genus and/or species level. The dentaries herein described pertains to “Scincomorpha” on the basis of the presence of a subdental ridge (Evans, 2008) and the well-defined sulcus dentalis they display (Augé and Rage, 2006; Rage and Augé, 2010). However, “Scincomorpha” is paraphyletic according to recent molecular-based and combined evidence phylogenetic analyses (e.g., Reeder et al., 2015; Simões et al., 2018). Following recent phylogenies of squamate reptiles (Vidal and Hedges, 2005), we here refer these specimens as pertaining to either an indeterminate Scinciformata or an indeterminate Laterata. The tooth morphology of UU NO1 1016 may recall the one of some Cordylidae Fitzinger, 1826, previously described in other, slightly older Greek localities (Georgalis et al., 2017, 2019b), but teeth of the specimen from Notio display either really light striae or even none at all. Moreover, even if it could pertain to Cordylidae, the fact that there is no other specimen more clearly referable to this taxon and that the posterior part of the dentary is missing make this identification doubtful. In addition, the trunk vertebrae do not show significant feature that would allow us to discriminate between Lacertidae and Scincidae, and the same holds true for the caudal vertebra, based on our current knowledge. Thus, they are also assigned as Scinciformata or Laterata indet.

Anguimorpha Fürbringer, 1900

Anguidae Gray, 1825

Anguinae Gray, 1825

Anguis Linnaeus, 1758

***Anguis* sp.**

Fig. 12A–E

Material: NO1: two trunk vertebrae (UU NO1 1015 and UU NO1 1026).

Description: Both vertebrae are of a relatively small size, with UU NO1 1015 having a centrum length of 3 mm (though highly fragmentary) and UU NO1 1026 being almost complete and having a centrum length of 4.7 mm (Fig. 12A–E). They are procoelous and their centrum is strongly dorsoventrally compressed. The centrum is flattened in ventral view and displays subparallel lateral margins in its posterior half. Both vertebrae show a light medial constriction of the neural arch. Their dorsal surface is provided with a well-developed neural spine.

Remarks: These specimens are referred to the genus *Anguis* on the basis of the dorsoventral compression of the centrum and the subparallel lateral margins of their ventral surface (Klembara, 1981; Čerňanský et al., 2019).

(non-*Anguis*) Anguinae indet.

Fig. 12F

Material: KO1highA: one osteoderm (UU KO1highA 1503).

Description: This osteoderm is large-sized and of roughly trapezoidal shape (Fig. 12F), with its preserved portion being 4 mm long and 4.7 mm wide. It is relatively thick and robust. The external surface displays two distinct portions, a smooth gliding surface and a vermicularly ornamented surface.

Remarks: *Anguis* osteoderms are recognized by their small overall size, their thinness and the absence of keel (Holman, 1998). Except for the absence of a keel, the only osteoderm present in the material hereby described does not match these characters. Therefore, the specimen from Komanos 1 is identified as a non-*Anguis* member of the Anguinae subfamily.

Anguidae indet.

Fig. 12G–K

Material: NO1: two caudal vertebrae (UU NO1 1027 and UU NO1 1075).

Description: These two caudal vertebrae are small-sized, with centrum length varying between 2.9 mm and 4 mm long (Fig. 12G–K). The centrum is also dorsoventrally compressed. The bases of fused hemapophyses are visible on the posteriormost portion of the ventral surface. No precondylar constriction can be observed and the neural arch displays a developed neural spine. The autotomy plane is present on the anterior end of the centrum of UU NO1 1027.

Remarks: These specimens are here identified as indeterminate Anguidae because of the dorsoventrally compressed centrum, the absence of precondylar constriction and the fused haemapophyses (Čerňanský et al., 2019). A more precise determination is not possible, even though caudal vertebrae of *Pseudopus* Merrem, 1820 tend to lose the autotomy plane (Etheridge, 1967; Čerňanský et al., 2019) in contrast with at least one of the specimens from Notio. Nevertheless, these specimens could likely pertain to anguines, the only anguid lineage clearly identified in Ptolemais localities and undisputedly present in the European Neogene as a whole (Georgalis et al., 2018a; but see Villa and Delfino, 2018, for a summary of the mention of other, unconfirmed anguid lineages).

(non-snake) Squamata indet.

Fig. 13

Material: TE1: four caudal vertebrae (UU TE1 1516). TE2: one femur (UU TE2 1505). NO1: one cloacal vertebra (UU NO1 1002); one trunk vertebra (UU NO1 1010); one heavily fragmented vertebra (UU NO1 1011).

Description: Trunk vertebra: The trunk vertebra UU NO1 1010 is procoelous and its centrum is 3 mm long and 1.7 mm wide (Fig. 13A–B). This specimen is in a poor preservation state. Indeed, only its ventral portion is present. The ventral surface is provided with two close subcentral ridges, defining a medial flat surface and flanked by a depressed area on each side. Cotyle and condyle are both elliptical. Moderately massive and dorsoventrally elongated synapophyses are preserved.

Cloacal vertebra: This procoelous vertebra is small-sized with a centrum 2.4 mm long and 2 mm wide (Fig. 13F–J). It is also relatively poorly preserved, with the major part of the dorsal portion being eroded and all of the structure present on the lateral sides being broken. It displays a morphology reminiscent of Anguidae. The centrum is not really elongated and shows a light medial constriction due to the presence of the bases of the broken sacral apophyses. The preserved dorsal surface displays a broken neural spine. Both dorsal and ventral sides of the vertebra display thin vessel-like imprints probably linked to taphonomic processes. In anterior view, the cotyle is elliptical and dorsoventrally compressed (it is almost two times wider than high), strongly transversally extended and roughly as wide as the neural canal. In posterior view, the condyle is also highly transversally extended. However, it is slightly wider than the neural canal, which is narrower and higher in its posterior part than in its anterior part. The ventral surface is relatively flat, sub-triangular and deprived of any particular structure.

Caudal vertebrae: These are small-sized and relatively poorly preserved, thus not preserving most of their original structures. They are elongated. On their ventral surface, they display a keel.

Fragment of vertebra: The vertebra UU NO1 1011 is highly fragmentary being represented by the left prezygapophysis, the size of which reaches 1.8 mm long. The prezygapophysis is oval in shape. Based on the size of this fragment, it can be assumed that the vertebra was moderately to large-sized.

Remarks: Due to their poor preservational state and in the absence of clear diagnostic features, the present remains are here identified as indeterminate lizards. It is possible that these remains pertain to any of the above described lizard taxa. In addition, the flattened centrum of UU NO1 1002 seems to recall the Anguidae-like morphology of the cloacal vertebrae known in the anguids *Anguis* and *Pseudopus* (Venczel, 2001; Rage and Bailon, 2005; Čerňanský et al., 2019). However, due to its preservational status, it cannot be confidently identified as such.

Serpentes Linnaeus, 1758

Alethinophidia Nopcsa, 1923

Caenophidia Hoffstetter, 1939

Colubridae Oppel, 1811

“Colubrinae” Oppel, 1811 (*sensu* Szyndlar, 1984, 1991a)

“Colubrinae” indet.

Fig. 14

Material: TE2: six trunk vertebrae (UU TE2 1514). NO1: nine trunk vertebrae (UU NO1 1013 [two], UU NO1 1030, UU NO1 1039–1044); one postcloacal vertebra (UU NO1 1029).

Description: The preservation of these vertebrae ranges from relatively good to rather poor (Fig. 14A–T). The vertebrae are generally small-sized (centrum length ranging approximatively between 2 to 4 mm), with the exception of specimens UU NO1 1039, UU NO1 1040 and UU NO1 1044 which stand out by their larger size (5 to 6 mm long) and are more robust. The centrum length/width ratio (abbreviated CL/NAW, sensu Szyndlar, 1984) of theses vertebrae range from 1.06 to 1.75 with a mean value of 1.37 ± 0.17. In anterior view (Fig. 14A, F, K), the zygosphene is thin and convex. The prezygapophyses are straight and rather not inclined neither ventrally nor dorsally. The prezygapophyseal processes are only preserved in UU NO1 1039, 1040 and 1042. They are well developed and extend anterolaterally. The cotyle is circular. The neural canal and the cotyle are roughly the same size with the exception of UU NO1 1042 where the former is slightly larger than the latter, suggesting that this vertebra might come from the anterior part of the vertebral column. In posterior view (Fig. 14B, G, L, Q), the neural arch is slightly compressed dorsoventrally. The condyle is circular. The zygantrum is either poorly preserved or absent on every specimen. In dorsal view (Fig. 14C, H, M, R), the prezygapophyses extend anterolaterally and the prezygapophyseal articular facets are oval. In ventral view (Fig. 14D, I, N, S), the centra are slightly longer than wide. Besides UU NO1 1029, which is a vertebra from the postcloacal region, thus provided with haemapophysis, the other vertebrae are provided with a narrow haemal keel. This structure originates close to the cotyle. In UU NO1 1040 and UU NO1 1042, it gradually enlarges toward the condyle. The postzygapophyses are not preserved in any specimen. In lateral view (Fig. 14E, J, O, T), the neural spine appears low, but it is generally broken. A light interzygapophyseal ridge is visible. Below this structure, a lateral foramen is present. When preserved, synapophyses are clearly divided into diapophyses and parapophyses. The postcloacal vertebra UU NO1 1029 is provided with relatively straight pleurapophyses, which are however broken.

Remarks. The vertebrae described here show the diagnostic feature of "Colubrinae", which is the presence of an haemal keel instead of an hypapophysis on the post-cervical region of the vertebral column (Szyndlar, 1991a), thus being distinguished from "Natricinae" among colubrids. It seems that the material pertains to two different "colubrine" groups. The general morphology of these vertebrae (except for UU NO1 1040) (e.g., lightly built, elongated centrum, size around 5 mm or smaller) seems to be more consistent with the informal group of "small-sized colubrines" (Szyndlar, 1984, 1991a). It is also worth noting that specimen UU NO1 1040 is larger and shows resemblance with the group of "large-sized colubrines" (Szyndlar, 1991a). Indeed, it displays features that recall *Malpolon* Fitzinger, 1826 (e.g., circular cotyle and long prezygapophyseal processes; Bailon, 1991; Szyndlar, 1991a). Due to its fragmentary nature, however, most of the diagnostic features are missing. Therefore, a tentative identification of this specimen is not given here.

"Natricinae" Bonaparte, 1838 (*sensu* Szyndlar, 1991b)

Natrix Laurenti, 1768

***Natrix* sp.**

Figs. 15–16

Material: VOR1: one trunk vertebra (UU VOR1 1501). VOR2: two trunk vertebrae (UU VOR2 1514 and UU VOR2 1522). VOR3: four trunk vertebrae (UU VOR3 1510, UU VOR3 1512 [two] and UU VOR3 1513). VOR3A: six trunk vertebrae (UU VOR3A 1507 [three], UU VOR3A 1508 [two] and UU VOR3A 1528). NO1: five trunk vertebrae (UU NO1 1062, UU NO1 1063, UU NO1 1065, UU NO1 1069 and UU NO1 1070).

Description: The size of these vertebrae is variable. The centrum length ranges from 3 to 5 mm and the centrum width ranges from 2.8 to 4 mm (Figs. 15–16). CL/NAW range from 1.07 to 2.00 (average: 1.43 ± 0.20). In dorsal view (Figs. 15A, F K, and 16A, F, K), the zygosphenal lip is slightly crenulated, displaying two prominent lateral lobes and a median one. The prezygapophyses extend anterolaterally. The prezygapophyseal articular facets are moderately large, oval and flattened. Some specimens (UU VOR2 1514 and UU VOR3 1510, among others) show a relatively short prezygapophyseal accessory process with a pointed tip. In ventral view (Figs. 15B, G and L and 16B, G, L), the centrum is elongated. A distinct hypapophysis is present, with its anteriormost portion being almost at the level of the cotyle. These specimens are provided with a subcentral foramen on each side of its hypapophysis. However, some vertebrae display only a subcentral foramen on a single side of their hypapophysis (i.e., UU VOR2 1522; Fig. 15G) or none at all (i.e., UU NO1 1070; Fig. 16 B). Postzygapophyseal articular facets are relatively small and elongated. In anterior view (Figs. 15C, H, M and 16C, H, M), the zygosphene is relatively thin and slightly convex. Prezygapophyses are straight and slightly dorsally oriented. The neural canal is subcircular and narrow. The cotyle is transversally extended and its ventral border is straight. The cotyle and the neural canal are almost of equal size. On each side of the cotyle, a large paracotylar foramen is present. The parapophyses do not seem to extend far beyond the ventral surface of the cotyle but this observation should be treated carefully as they are eroded. The parapophyseal processes appear strong and anteriorly directed. In posterior view (Figs. 15D, I, N and 16D, I, N), the neural arch is slightly depressed. Several distinct foramina are present on the edges of the postzygapophyses. The condyle is circular. In lateral view (Figs. 15E, J, O and 16E, J, O), a neural spine is present but this structure is partially broken on every specimen. Therefore, its height and morphology cannot be precisely assessed. The neural spine is as long as two thirds of the length of the neural arch. A well-defined interzygapophyseal ridge is present. Below the latter, lateral foramina are present. The hypapophysis is sigmoid, relatively short and its posterior end does not extend past the condyle. The synapophyses are divided into well-individualized diapophyses and parapophyses that show similar development.

Remarks: The vertebrae here described are attributed to the genus *Natrix* on the basis of the presence of a sigmoid hypapophysis, strong and antero-ventrally directed parapophyseal processes, a straight ventral border of the cotyle and the general morphology of the preserved structures that are reminiscent of this genus (Szyndlar, 1984, 1991b; Rage and Szyndlar, 1986). Some of the specimens show features that are reminiscent of *Natrix longivertebrata* Szyndlar, 1984 such as dorsoventrally flattened and stout prezygapophyseal accessory processes, parapophyseal processes strong and clearly projected anteriorly beyond the lower lip of the cotyle (Szyndlar, 1984, 1991b; Rage and Szyndlar, 1986; Rage and Bailon, 2005). However, the features that are considered to be diagnostic of this taxon are somewhat widespread in *Natrix*, thus they might not be completely reliable. Moreover, the vertebrae from Ptolemais are not as elongated as in *N. longivertebrata.* Indeed, the centrum length/width ratio of the vertebrae from Ptolemais is out of the range known in specimens from the Upper Pliocene (MN 16) of Rebielice Krolewskie I, Poland, the type locality of *N. longivertebrata.* Indeed, in the original description of this species, the given CL/NAW range from 1.76 to 2.22 with a mean value of 1.92 ± 0.12. However, the CL/NAW values of the Ptolemais material range from 1.07 to 2.00 (mean value of 1.43 ± 0.20). As such, the herein described material is identified as *Natrix* sp.

“Natricinae” indet.

Fig. 17

Material: TE1: one vertebra (UU TE1 1514). TE2: eight vertebrae (UU TE2 1511, UU TE21513 [five] and UU TE2 1516 [two]). NO1: nine vertebrae (UU NO1 1014 [four], UU NO1 1034, UU NO1 1064, UU NO1 1066, UU NO1 1067 and UU NO1 1068).

Description: These vertebrae (Fig. 17A–O) are relatively poorly preserved, the smallest fragment (UU NO1 1014) consisting only in a portion of centrum and neural arch reaching around 2 mm in length and the largest one (UU NO1 1064) being almost complete and around 4 mm long. They display a neural spine, which is usually broken. In anterior view, the zygosphene is thin, straight and wider than the cotyle. The neural arch is slightly depressed and the neural canal is subcircular or oval. The prezygapophyseal accessory processes are broken on every specimen. In lateral view, there is a straight interzygapophyseal ridge. These vertebrae, despite their variable preservation status, all display a sigmoid hypapophysis or the remnants of that structure on the middle part of the ventral surface of their centrum.

Remarks: The overall poor preservation status of these vertebrae and the lack of clear diagnostic features prevent from any confident generic and specific identification. However, it is still possible to attribute them to "Natricinae" morphotype in regards to their hypapophysis and the sigmoid shape of the latter (Szyndlar, 1984, 1991b). Two other snake families that display the persistent hypapophysis throughout the vertebral column were widespread in the Miocene and Pliocene of Greece: Elapidae Boié, 1827 and Viperidae Gray, 1825 (of the "Oriental vipers complex"). The vertebrae of the former (Elapidae) are more robust, provided with laterally compressed hypapophysis and a low neural spine (Čerňanský et al., 2015). On the other hand, the latter (Viperidae of the "Oriental vipers complex") is provided with vertebrae that display a short centrum, relatively wide condyles and cotyles, a longer and straighter hypapophysis, posteriorly depressed neural arches and higher neural spines, ventrally oriented parapophyseal processes and postzygapophyses that are highly laterally extended (Szyndlar, 1991b; Georgalis et al., 2016a). Therefore, a referral to either elapids or viperids can here be discarded on the basis of the elongated centra and the apparently low and short hypapophyses of the vertebrae here described. That being said, it cannot be concluded with certainty whether these specimens in fact pertain to the same taxon as the above described specimens *Natrix* sp. or represent a distinct "natricine" form.

Colubridae indet.

Fig. 18

Material: TE2: one right pterygoid (UU TE2 1510). NO1: one vertebra (UU NO1 1028); one vertebra (UU NO1 1031).

Description: Pterygoid: This specimen is 5.5 mm long in its anteroposterior direction. It is much fragmentary. Ventrally, it shows several teeth that are slightly hooked toward the back of the pterygoid and disposed on a straight tooth ramus (Fig. 18A–C). This right pterygoid displays a partially broken anteriorly directed ectopterygoid process. On its dorsal surface, it displays a strong pterygoid crest, whereas its ventral surface is flat. Even though this specimen is fragmentary, it seems to widen in its anteriormost part.

Vertebrae: The centrum of UU NO1 1028 is 2.7 mm long and 2.1 mm wide, whereas UU NO1 1031 is quite larger with a 4 mm long and 2.8 mm wide centrum. A neural spine is present on their neural arch. However, the ventral side is strongly damaged in both specimens; thus, if any hypapophysis was present in origin, it cannot be concluded.

Remarks: The Tomea Eksi 2 pterygoid does not display much diagnostic features. Its anterior part being wider than its posterior part is a feature known in Colubridae sensu lato

(Blain et al., 2013). In addition, its morphology, the anteriorly directed ectopterygoid process and the well-defined pterygoid crest present on the dorsal surface of the bone are consistent with structures known in colubrids (Szyndlar, 1984). Therefore, this specimen is considered as an indeterminate Colubridae. This specimen is until now the only pterygoid that has been found in the Ptolemais material, excluding any comparison. A more precise identification based on the other remains from Tomea Eksi 2 cannot be achieved here as both "Colubrinae" and "Natricinae" were identified in this locality. Concerning the Notio vertebrae, the presence of a neural spine and the CL/NAW ratio allow attributing these remains to Colubridae. However, their preservational status and the same issue above raised for the pterygoid (that is, the presence of both subgroups of the family in Notio) hinder any identification more precise than at family level.

Caenophidia indet.

Fig. 19

Material: TE1: two trunk vertebrae (UU TE1 1513 and UU TE1 1534). TE2: 12 trunk vertebrae (UU TE2 1512 [five] and UU TE2 1515 [seven]); one caudal vertebra (UU TE2 1517). TE3: one trunk vertebra (UU TE3 1520). VOR3: three trunk vertebrae (UU VOR3 1509, UU VOR3 1511 and UU VOR3 1525). VOR3A: five trunk vertebrae (UU VOR3A 1505 [two] and UU VOR3A 1506 [three]). VOR8: one trunk vertebra (UU VOR8 1501). NO1: two trunk vertebrae (UU NO1 1033 and UU NO1 1035).

Remarks: All of these vertebrae (Fig. 19A–O), with the exception of UU TE2 1517, are poorly preserved and/or do not display any clear characteristic that can be used to precisely identify them. Only the presence of a neural spine on the neural arches excludes an attribution to Scolecophidia Duméril et Bibron, 1844, leaving only the Alethinophidia as a valid taxonomic option. The herein described material does not include any vertebra that could be identified as Boidae Gray, 1825 or as Aniliidae sensu lato Fitzinger, 1826. Vertebrae of the former group are provided with a wide and short centrum with centrum lengths usually wider than the neural arch width (Szyndlar, 1991a; Augé and Rage, 2006; Georgalis and Scheyer, 2019). The latter is a group of primitive snakes, in which vertebrae are strongly depressed and deprived of paracotylar foramina, both neural spine and haemal keel are reduced and the synapophyses are not differentiated into diapophyses and parapophyses (Hoffstetter & Gasc, 1969; Bailon, 1988, 1991). Considering the widespread presence of "colubrines", natricines, viperids, and elapids in the Greek Neogene (e.g., Georgalis et al., 2016a, c, 2017, 2018a, 2019a, b), this Ptolemais indeterminate material could pertain to any of these clades. We accordingly refer it solely as Caenophidia indet.

Alethinophidia indet.

Fig. 20

Material: NO1: one trunk vertebra (UU NO1 1012); two trunk vertebrae (UU NO1 1032).

Remarks: The specimens presented here are very poorly preserved (Fig. 20A–C). The ventral part is the only portion of these vertebrae that is preserved. In ventral view, they display an haemal keel. In anterior view, the condyle is slightly depressed. In Scolecophidia, the condyles and cotyles are strongly flattened; thus, although fragmented, the few characters displayed by these specimens exclude an attribution this taxon. Therefore, these vertebrae are identified as Alethinophidia indet. Nevertheless, the absence of haemapophyses and / or pleurapophyses denotes that they pertain to the precloacal portion of the vertebral column.

5. Discussion

Despite its poor preservational status, the herein described fossil material of amphibians and reptiles from the area of Ptolemais, in northwestern Greece, adds to our understanding of Neogene herpetofaunas of southeastern Europe. Especially, the 12 different localities within the Ptolemais area that yielded amphibian and reptile remains, ranging between MN 13 and MN 15, offer an important insight in changes of herpetofaunal assemblages during the transition between the late Miocene and the early Pliocene, a time lapse that is known to have been crucial for the evolution of European herpetofaunas (see Georgalis et al. 2019b). Amphibian assemblages in Ptolemais are of low diversity, with at least two frog taxa identified, whereas reptiles are apparently more diverse, being represented by at least one turtle, four lizards, and two snake taxa.

The identification of the genus *Latonia* from Ptolemais confirms that this genus was widespread in Greece during the Neogene, corroborating previous recent studies that described remains of this frog from the area (Georgalis et al., 2019a, b). Furthermore, the abundance and continuous presence of *Latonia* in the Ptolemais area (the genus is recovered from all the 12 localities treated in this paper; Table 1) demonstrates that this frog persisted practically unaffected during the crucial latest Miocene / earliest Pliocene interval. Indeed, it is much possible that all these *Latonia* specimens pertain to the same species, however, the presence of a potential, second species remains to be securely excluded only upon the recovery of more complete, diagnostic finds. *Rana* is a genus that still occurs in the extant herpetofauna of the Greek mainland. The identification of *Rana* in Ptolemais marks its oldest occurrence in the area. Interestingly also, similarly to the case of *Latonia* discussed above, *Rana* is known as well from both the late Miocene and early Pliocene of the Ptolemais area, demonstrating that the genus “crossed” the Mio-Pliocene boundary. Not a lot can be said about the indeterminate anurans from Ptolemais and as such, the presence of a third frog taxon from these localities cannot be excluded, also considering the peculiar morphology of the sacral vertebra UU TE1 1519.

The presence of a testudinid in the Ptolemais area is important as it testifies that *Testudo* or *Testudo*-like related forms were abundant during the Greek Neogene. Already known from Greece since the second half of the 19th century (Gaudry, 1862–1867), fossils of testudinids have since been found from several different localities of the country (Georgalis and Kear, 2013; Vlachos et al., 2015; Garcia et al., 2016). The rather incomplete nature of the single known specimen from Ptolemais does not permit a secure generic attribution, defying thus any further taxonomic conclusion. As for the indeterminate testudinoids, they are also too fragmentary to permit any identification; as such, it cannot be confirmed whether certain of them pertain to geoemydids, a testudinoid lineage that is abundant in the Neogene of Greece (e.g., Georgalis and Kear, 2013; Vlachos et al., 2015; Georgalis et al., 2019b).

Lizards are poorly documented from Ptolemais, having been recovered solely from four among the 12 fossiliferous localities treated herein. Of special interest is the presence of scincids, which ranks among the only two formally described fossil occurrences of this lineage in Greece (the other being from the latest Miocene / earliest Pliocene of Maramena; Georgalis et al., 2019b), despite the wide range and relatively high diversity of this group in extant herpetofauna of the country (Sindaco and Jeremčenko, 2008). As is a common fact with lacertid fragmentary fossil remains, which usually do not afford taxonomic referral even to the genus level, the occurrences of this group in Ptolemais (known only from two late Miocene [MN 13] and one early Pliocene [MN 15] localities from the area) do not add any significant input into our understanding of the evolution and precise relationships of these lizards. Furthermore, lacertids are abundant squamates in the Greek Neogene fossil record, despite the fact that their fossil remains have been only relatively recently described (e.g., Richter, 1995; Georgalis et al., 2017, 2019a, b; Vasileiadou et al., 2017), whereas they are also the dominant and most diverse group of reptiles in the extant fauna of the country (Sindaco and Jeremčenko, 2008). Anguids are also relatively common finds in the Greek Neogene fossil record (Richter, 1995; Georgalis et al., 2017, 2019 a, b; see also the supplementary material in Villa and Delfino, 2018) and the Ptolemais sample concords with this fact, as anguids are found in two localities across the Mio-Pliocene boundary (Komanos 1 high A [MN 13] and Notio 1 [MN 15]). What appears most interesting though in the Ptolemais anguid record is the presence of *Anguis* in the early Pliocene of the Notio 1 locality. Indeed, even though *Anguis* is a genus that still resides in that area (Sindaco and Jeremčenko, 2008; Valakos et al., 2008), its fossil record in the region is extremely poor, with the herein described material constituting the second only record of this genus in the Greek area, adding to the recently described congeneric remains from the latest Miocene / earliest Pliocene (MN 13 / 14) of Maramena, also from northern Greece (Georgalis et al., 2019b).

Snakes in the Ptolemais fossil material consist of abundant remains, having been recovered from nine among the 12 studied localities. However, they are all rather fragmentary, usually not allowing precise taxonomic assignments. Nevertheless, “colubrines” and the natricine genus *Natrix* can be identified. “Colubrines” are mostly represented by rather small vertebrae that apparently pertain to a small-sized form, but a few other specimens denote also the presence of a larger taxon / morphotype. Whether this size ranges differences reflects also some kind of taxonomic distinctiveness or simply ontogenetic variation cannot be evaluated on the basis of the existing fragmentary remains. The presence of *Natrix* in Ptolemais adds to the known Neogene records of the genus in Greece, being also known from the late Miocene (MN 13) of Ano Metochi (Georgalis et al., 2017) and the latest Miocene / earliest Pliocene (MN 13 / 14) of Maramena (Szyndlar, 1991b, 1995; Georgalis et al., 2019b).

Natrix is currently widespread in the extant snake herpetofauna of the country (Sindaco and Jeremčenko, 2008; Valakos et al., 2008).

6. Conclusions

The herpetofauna of the Ptolemais area in northern Greece described herein adds to our current knowledge of southeastern European amphibians and reptiles during the Neogene. The amphibian and reptile specimens originate from 12 different but proximate localities of the Ptolemais area, spanning from the late Miocene (MN 13) to the early Pliocene (MN 15). Amphibians include exclusively frogs, consisting of the alytid *Latonia* and the ranid *Rana*, whereas several indeterminate anuran bones were also recognized. Reptiles comprise the testudinid cf. *Testudo*, indeterminate turtles, scincids, lacertids, at least two taxa of anguines (including the relatively rare as Neogene fossil *Anguis*), "colubrines", the "natricine" *Natrix*, plus several indeterminate squamate bones. Both *Latonia* and *Rana* existed across the Mio-Pliocene boundary in the area, as they are found from both late Miocene and early Pliocene localities of Ptolemais. The record of *Anguis* constitutes one among only a few such occurrences of this genus in the Neogene of the Eastern Mediterranean.

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References

Augé, M., 2005. Evolution des lézards du Paléogène en Europe. Mémoires du Muséum national d'Histoire naturelle. Vol. 192. Paris: 369 pp.

Augé, M., Hervet, S., 2009. Fossil lizards from the locality of Gannat (late Oligocene–early Miocene, France) and a revision of the genus *Pseudeumeces* (Squamata, Lacertidae). Palaeobiodiversity and Palaeoenvironments. 89(3–4):191–201.

Augé, M., Rage, J.C., 2006. Herpetofaunas from the upper Paleocene and lower Eocene of Morocco. Annales de Paléontologie. 92(3):235–253.

Bailon, S., 1988. Un Aniliidé (Reptilia, Serpentes) dans le Pliocène supérieur européen. Comptes Rendus de l'Académie des Sciences, Paris, 306(II):1255-1258.

Bailon, S., 1991. Amphibiens et reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes. PhD dissertation. Université de Paris VII, Paris.

Bailon, S., 1999. Différenciation ostéologique des anoures (Amphibia, Anura) de France. In: J. Desse, N. Desse-Berset (ed.). Fiches d'ostéologie animale pour l'Archéologie, Série C: Varia, 1. Antibes: APDCA: 1–41.

Barahona, F., Barbadillo, L.J., 1997. Identification of some Iberian lacertids using skull characters. Revista Española de Herpetología. 11:47–62.

Batsch, AJGC., 1788. Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien, für akademische Vorlesungen entworfen, und mit dennöthigsten Abbildungen versehen, Erster Theil. Allgemeine Geschichte der Natur; besondre der Saügthiere, Vögel, Amphibien und Fische. Jena. Akademische Buchhandlung.

Bibron, G., Bory de Saint-Vincent, J.B., 1833. Expédition scientifique de Morée, Zoologie Reptiles et poissons. Polypiers. Paris, Strasbourg, F.G. Levrault

Biton, R., Boistel, R., Rabinovich, R., Gafny, S., Brumfeld, V., Bailon, S., 2016. Osteological observations on the Alytid Anura *Latonia nigriventer* with comments on functional morphology, biogeography, and evolutionary history. Journal of Morphology. 277(9):1131–1145.

Biton, R., Geffen, E., Vences, M., Cohen, O., Bailon, S., Rabinovich, R., Malka, Y., Oron, T., Boistel, R., Brumfeld, V. Gafny, S. 2013. The rediscovered Hula painted frog is a living fossil. Nature Communications. 4:1959.

Blain, H.A., Agustí, J., López-García, J.M., Haddoumi, H., Aouraghe, H., Hammouti, K.E., Pérez-Gonzàlez, A., Chacón, M.G., Sala, R., 2013. Amphibians and squamate reptiles from the late Miocene (Vallesian) of eastern Morocco (Guefaït-1, Jerada Province). Journal of Vertebrate Paleontology. 33(4):804–816.

Blain, H.A., Lozano-Fernandez, I., Böhme, G., 2015. Variation in the ilium of central European water frogs *Pelophylax* (Amphibia, Ranidae) and its implications for species-level identification of fragmentary anuran fossils. Zoological Studies. 54(5):1–9.

Boie, F., 1827. Bemerkungen über Merrem's Versuch eines Systems der Amphibien. 1. Lieferung: Ophidier. Isis von Oken, 20, 508–566.

Bonaparte, C.L., 1838. *Synopsis vertebratorum systematis. Amphibiorum Tabula Analytica.* Nuovi Annali delle Scienze Naturali, Bologna. 1:391–397.

Camaiti, M., Villa, A., Wencker, L.C.M., Bauer, A.M., Stanley, E.L., Delfino, M., 2019. Descriptive osteology and patterns of limb loss in the European limbless skink *Ophiomorus punctatissimus* (Bibron and Bory de St.Vincent, 1833) (Squamata, Scincidae). Journal of Anatomy. 235(2):313-345.

Caputo, V., 2004. The cranial osteology and dentition in the scincid lizards of the genus *Chalcides* (Reptilia, Scincidae). Italian Journal of Zoology. 71(S2):35–45.

Čerňanský, A., Augé, M., 2013. New species of the genus *Plesiolacerta* (Squamata: Lacertidae) from the upper Oligocene (MP28) of Southern Germany and a revision of the type species *Plesiolacerta lydekkeri*. Palaeontology. 56(1):79–94.

Čerňanský, A., Rage, J.C., Klembara, J., 2015. The Early Miocene squamates of Amöneburg (Germany): the firsts stages of modern squamates in Europe. Journal of Systematic Palaeontology. 13(2):97–128.

Čerňanský, A., Yaryhin, O., Ciceková, J., Werneburg, I., Hain, M., Klembara, J., 2019. Vertebral comparative anatomy and morphological differences in anguine lizards with a special reference to *Pseudopus apodus*. Anatomical Record. 302:232–257.

Colombero, S., Angelone, C., Bonelli, E., Carnevale, G., Cavallo, O., Delfino, M., Giuntelli, P., Mazza, P., Pavia, G., Pavia, M., Repetto, G., 2014. The upper Messinian assemblages of fossil vertebrate remains of Verduno (NW Italy): another brick for a latest Miocene bridge across the Mediterranean. Neues Jahrbuch fur Geologie und Palaontologie Monatshefte. 272(3):287–324.

Cope, E.D., 1868. On the origin of genera. Proceedings of the Academy of Natural Sciences of Philadelphia. 20:242–300.

Crawford, N.G., Parham, J.F., Sellas, A.B., Faircloth, B.C., Glenn, T.C., Papenfuss, T.J., Henderson, J.B., Hansen, M.H., Simison, W.B., 2015. A phylogenomic analysis of turtles. Molecular phylogenetics and evolution, 83:250–257.

Duméril, A.M.C., Bibron, G., 1844. Erpétologie générale: ou, Histoire naturelle complète des reptiles. Vol. 6. Roret.

Đurić, D., 2016. The Early Miocene herpetofauna (Amphibia and Squamata) from Sibnica, Serbia. In: Z. Marković, and M. Milivojević, (ed.). The Neogene of Sibnica and vicinity (Levač basin, Central Serbia) Part 1. Natural History Museum in Belgrade Special issue: 57–61.

Etheridge, R., 1967. Lizard caudal vertebrae. Copeia. 1967(4):699–721.

Evans, S. E., 2008. The skull of lizards and tuatara. In: C. Gans, A. Gaunt, K. Adler, (ed.). Biology of the Reptilia. Vol. 20. Ithaca: Academic Press: 347 pp.

Fischer von Waldheim, G., 1813. Zoognosia. Tabulis Synopticis Illustrata, in Usum Prælectionum Academiæ Imperialis Medico-Chirurgicæ Mosquensis Edita. Ed. 3.Vol. 1. Moscow: Nicolai Sergeidis Vsevolozsky.

Fitzinger, L.J.F.J., 1826. Neue Classification der Reptilien, nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisseder Reptilien-Sammlung des k.k. Zoologischen Museum zu Wien. Wien: J.G.Hübner Verlagen.

Fitzinger, L.J.F.J., 1843. Systema Reptilium, fasciculus primus. Wien: Braumüller et Seidel.

Forskål, P., 1775. Descriptiones Animalium: Avium, Amphibiorum, Piscium, Insectorum, Vermium; quae in Itinere Orientali Observavit. Post mortem auctoris edidit Carsten Niebuhr. Hauniae [Copenhagen]: Mölleri.

Friant, M., 1944. Caractères anatomiques d'un batracien oligocène de la Limagne, le *Prodiscoglossus Vertaizoni* nov. gen. nov. sp. Comptes rendus hebdomadaires séances de l'Académie des Sciences. 219:561–562.

Fürbringer, M., 1900. Zur vergleichenden anatomie des Brustschulterapparates und der Schultermuskeln. Jenaische Zeitschrift für Naturwissenschaft. 34:215–718.

Garcia, G., Kostopoulos, D.S., Valentin, X., Koufos, G.D., 2016. Testudines. In: G.D. Koufos and D.S. Kostopoulos (ed.). Palaeontology of the upper Miocene vertebrate localities of Nikiti (Chalkidiki Peninsula, Macedonia, Greece). Geobios 49:23–27.

Gaudry, A., 1862–1867. Animaux fossiles et géologie de l'Attique, d'après les recherches faites en 1855–56 et 1860. Savy, Paris. 474 pp.

Gauthier, J.A., Kearney, M., Maisano, J.A., Rieppel, O., Behlke, A.D., 2012. Assembling the squamate tree of life: perspectives from the phenotype and the fossil record. Bulletin of the Peabody Museum of Natural History, 53(1):3–309.

Georgalis, G.L., Joyce, W.G., 2017. A review of the fossil record of Old World turtles of the clade *Pan-Trionychidae*. Bulletin of the Peabody Museum of Natural History. 58(1):115–209.

Georgalis, G.L., Kear, B.P., 2013. The fossil turtles of Greece: an overview of taxonomy and distribution. Geobios. 46(4):299–311.

Georgalis, G.L., Scheyer, T.M., 2019. A new species of *Palaeopython* (Serpentes) and other extinct squamates from the Eocene of Dielsdorf (Zurich, Switzerland). Swiss Journal of Geosciences, https://doi.org/10.1007/s00015-019-00341-6

Georgalis, G.L., Velitzelos, E., Velitzelos, D., Kear, B.P., 2013. *Nostimochelone lampra* gen. et sp. nov., an enigmatic new podocnemidoidean turtle from the lower Miocene of northern Greece. In: D. Brinkman, P. Holroyd, J. Gardner (ed.). Morphology and evolution of turtles: papers in honor of Eugene S. Gaffney. Vol. 3 Pleurodires. Dordrecht (The Netherlands): Springer: 277–287.

Georgalis, G.L., Szyndlar, Z., Kear, B.P., Delfino, M. 2016a. New material of *Laophis crotaloides*, an enigmatic giant snake from Greece, with an overview of the largest fossil European vipers. Swiss Journal of Geosciences. 109:103–116.

Georgalis, G.L., Villa, A., Delfino, M., 2016b. First description of a fossil chamaeleonid from Greece and its relevance for the European biogeographic history of the group. The Science of Nature. 103:12.

Georgalis, G.L., Villa, A., Vlachos, E., Delfino, M., 2016c. Fossil amphibians and reptiles from Plakias, Crete: a glimpse into the earliest late Miocene herpetofaunas of southeastern Europe. Geobios. 49(6):433–444.

Georgalis, G.L., Villa, A., Delfino, M., 2017. Fossil lizards and snakes from Ano Metochi – a diverse squamate fauna from the latest Miocene of northern Greece. Historical Biology. 29(6):730–742.

Georgalis, G.L., Rage, J.C., de Bonis, L., Koufos, G., 2018a. Lizards and snakes from the late Miocene hominoid locality of Ravin de la Pluie (Axios Valley, Greece). Swiss Journal of Geosciences. 111:169–181.

Georgalis, G.L., Villa, A., Delfino, M., 2018b. The last amphisbaenian (Squamata) from continental Eastern Europe. Annales de Paléontologie. 104:155–159.

Georgalis, G.L., Villa, A., Ivanov, M., Roussiakis, S., Skandalos, P., Delfino, M., 2019a. Early Miocene herpetofaunas from the Greek localities of Aliveri and Karydia –

bridging a gap in the knowledge of amphibians and reptiles from the early Neogene of southeastern Europe. Historical Biology. 31:1045–1064.

Georgalis, G.L., Villa, A., Ivanov, M., Vasilyan, D., Delfino, M., 2019b. Fossil amphibians and reptiles from the Neogene locality of Maramena (Greece), the most diverse European herpetofauna at the Miocene / Pliocene transition boundary. Palaeontologia Electronica.

Gmelin, J.F., 1789. Caroli a Linne, Systema Naturae perregna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed.13. Tom. I. Pars III. Leipzig: G.E. Beer.

Gray, J.E., 1825. A synopsis of the genera of Reptiles and Amphibia, with a description of some new species. Annals of Philosophy, Series. 2(10):193–217.

Hedges, S.B., 2014. The high-level classification of skinks (Reptilia, Squamata, Scincomorpha). Zootaxa. 3765(4):317–338.

Hervet, S., 2000. Tortues du Quaternaire de France: critères de détermination, répartitions chronologique et géographique. Mésogée. 58:3–47.

Hoffstetter, R., 1939. Contribution à l'étude des Elapidae actuels et fossiles et de l'ostéologie des ophidiens. Publications du Musée des Confluences. 15(1):1–78.

Hoffstetter, R., Gasc, J.P., 1969. Vertebrae and ribs of modern reptiles. In: C. Gans, A. d'ABellairs, T. Parsons (ed.). Biology of the Reptilia. Vol. 1. Morphology A. London: Academic Press: 201–310.

Holman, J.A., 1998. Pleistocene amphibians and reptiles in Britain and Europe. New-York: Oxford University Press: 256 pp.

Hordijk, K., de Bruijn, H., 2009. The succession of rodent faunas from the Mio/Pliocene lacustrine deposits of the Florina-Ptolemais-Servia Basin (Greece). Hellenic Journal of Geosciences. 44:21–103.

Hossini, S., 1993. A new species of *Latonia* (Anura, Discoglossidae) from the lower Miocene of France. Amphibia-Reptilia. 14(3):237–245.

Kalaitzidis, S., Bouzinos, A., Papazisimou, S., Christanis, K., 2004. A short-term establishment of forest fen habitat during Pliocene lignite formation in the Ptolemais Basin, NW Macedonia, Greece. International Journal of Coal Geology. 57(3-4):243–263.

Khosatzky, L.I., Młynarski, M., 1966. Fossil tortoises of the genus *Geoemyda* Gray, 1834 (s. lat.) of Europe. Acta Zoologica Cracoviensia. 11:397–417.

Klembara, J., 1981. Beitrag zur kenntnis der subfamilie Anguinae (Reptilia, Anguidae). Acta Universitatis Carolinae, Geologica. 2:121–168.

Kloosterboer-van Hoeve, M.L., 2000. Cyclic changes in the late Neogene vegetation of northern Greece. PhD thesis, Utrecht University, Utrecht. 131 pp.

Kloosterboer-van Hoeve, M.L., Steenbrink, J., Brinkhuis, H., 2001. A short-term cooling event, 4.205 million years ago, in the Ptolemais Basin, northern Greece. Palaeogeography, Palaeoclimatology, Palaeoecology. 173(1-2):61–73.

Kloosterboer-van Hoeve, M.L., Steenbrink, J., Visscher, H., Brinkhuis, H., 2006. Millennial-scale climatic cycles in the Early Pliocene pollen record of Ptolemais, northern Greece. Palaeogeography, Palaeoclimatology, Palaeoecology. 229(4):321–334.

Kosma, R., 2004. The dentition of recent and fossil Scincomorphan lizards (Lacertilia, Squamata) – Systematics, Functional Morphology, Palaeoecology. Unpublished Ph.D. thesis, University of Hannover.

Lartet, E., 1851. Notice sur la Colline de Sansan, suivie d’une récapitulation des diverses espèces d’animaux vertébrés fossiles, trouvés soit à Sansan, soit dans d’autres gisements du terrain tertiaire miocène dans le bassin Sous-Pyrenéen. Auch: J.A. Portes.

Laurenti, J.N., 1768. Specimen medicum, exhibens synopsin reptilium emendatam cum experimentis circa venena et antidota reptilium austriacorum. Vienna (Austria): Joan Thomae.

Linnaeus, C., 1758. Systema naturæ per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Tomus 1., Pars 1. Stockholm: Laurentii Salvius.

Lynch, J.D., 1969. Evolutionary relationships of the frog family Leptodactylidae. PhD dissertation. The University of Kansas, Lawrence, KS.

Merrem, B., 1820. Versuch eines systems der amphibian. Krieger.

Mendelssohn, H., Steinitz, H., 1943. A new frog from Palestine. Copeia. 1943(4):231–233.

Meyer H. v., 1843. Mittheilung an professor Bronn gerichtet. Neues Jahrbuch für Mineralogie, Geognosie. 1843:579–590.

Nopcsa, F., 1923. *Eidolosaurus* und *Pachyophis*. Zwei neue Neocom-Reptilien. Palaeontographica. 65:99–154.

Oppel, M., 1811. Die ordnungen, familien und gattungen der Reptilien als prodom einer naturgeschichte derselben. München: Joseph Lindauer Verlag.

Pyron, R.A., Wiens, J.J., 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. Molecular phylogenetics and evolution, 61(2):543–583.

Rafinesque, C.S., 1814. Fine del Prodromo d'Erpetologia Siciliana. Specchio delle Scienze, o Giornale Enciclopedico di Sicilia. 2:102–104.

Rage, J.C., 1974. Les batraciens des gisements quaternaires européens. Détermination ostéologique. Publications de la Société Linnéenne de Lyon. 43(8):276–289.

Rage, J.C., Augé, M., 2010. Squamate reptiles from the middle Eocene of Lissieu (France). A landmark in the middle Eocene of Europe. Geobios. 43(2):253–268.

Rage, J.C., Bailon, S., 2005. Amphibians and squamate reptiles from the late early Miocene (MN4) of Béon 1 (Montréal-du-Gers, southwestern France). Geodiversitas. 27(3):413–441.

Rage, J.C., Roček, Z., 2003. Evolution of anuran assemblages in the Tertiary and Quaternary of Europe, in the context of palaeoclimate and palaeogeography. Amphibia-Reptilia, 24:133–167

Rage, J.C., Szyndlar Z. 1986. *Natrix longivertebrata* from the European Neogene, a snake with one of the longest known stratigraphic ranges. Neues Jahrbuch fur Geologie und Palaontologie Monatshefte. 1986:56–64.

Ratnikov, V.Y., 2001. Osteology of Russian toads and frogs for paleontological researches. Acta Zoologica Cracoviensa. 44(1):1–23.

Reeder, T.W., Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Wood, P.L. Jr., Sites, J.W. Jr., Wiens, J.J., 2015. Integrated analyses resolve conflicts over squamate reptile phylogeny and reveal unexpected placements for fossil taxa. PLoS ONE, 10: e0118199.

Richter, A., 1994. Lacertilia aus der Unteren Kreide von Uña und Galve (Spanien) und Anoual (Marokko). Fachbereich Geowissenschaften, FU Berlin.

Richter, A., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 3. Lacertilia (Squamata, Reptilia). Münchner Geowissenchaften Abhandlungen 28:35–38.

Roček, Z., 1994. Taxonomy and distribution of Tertiary Discoglossids (Anura) of the Genus *Latonia* v. Meyer,1843. Géobios. 27(6):717–751.

Roček, Z., 2013. Mesozoic and Tertiary Anura of Laurasia. Palaeobiodiversity and Palaeoenvironments. 93:397–439.

Sen, S., Delfino, M., Kazanci, N., 2017. Çeştepe, a new early Pliocene vertebrate locality in Central Anatolia and its stratigraphic context. Annales de Paléontologie. 103(2):149–163.

Schoepff, I.D., 1792. Historia testudinum iconibus illustrata. [part 1]. J.J. Palm, Erlangae [=Erlangen]. xii + 136 pp.

Simões, T.R., Caldwell, M.W., Tałanda, M., Bernardi, M., Palci, A., Vernygora, O., Bernardini, F., Mancini, L., Nydam, R.L., 2018.The origin of squamates revealed by a Middle Triassic lizard from the Italian Alps. Nature. 557:706–709.

Sindaco, R., Jeremčenko, V., 2008. The Reptiles of the Western Palearctic. Vol.1. Annotated Checklist and Distributional Atlas of the Turtles, Crocodiles, Amphisbaenians and Lizards of Europe, North Africa, Middle East and Central Asia. Monografie della Societas Herpetologica Italica I, Belvedere, Latina.

Steenbrink, J., Hilgen, F.J., Krijgsman, W., Wijbrans, J.R., Meulenkamp, J.E., 2006. Late Miocene to Early Pliocene depositional history of the intramontane Florina–Ptolemais–Servia Basin, NW Greece: Interplay between orbital forcing and tectonics. Palaeogeography, Palaeoclimatology, Palaeoecology. 238(1-4):151–178.

Steenbrink, J., Van Vugt, N., Hilgen, F.J., Wijbrans, J.R., Meulenkamp, J.E., 1999. Sedimentary cycles and volcanic ash beds in the lower Pliocene lacustrine succession of Ptolemais (NW Greece): discrepancy between 40Ar/39Ar and astronomical ages. Palaeogeography, Palaeoclimatology, Palaeoecology. 152(3-4):283–303.

Steenbrink, J., Van Vugt, N., Kloosterboer-van Hoeve, M.L., Hilgen, F.J., 2000. Refinement of the Messinian APTS from sedimentary cycle patterns in the lacustrine Lava section (Servia Basin, NW Greece). Earth and Planetary Science Letters. 181(3–4):161–173.

Syromyatnikova, E., 2016. Anurans of the Tagay locality (Baikal lake, Russia; Miocene): Bombinatoridae, Hylidae, and Ranidae. Russian Journal of Herpetology, 23(2):145–157.

Syromyatnikova, E., Roček, Z., 2018. New *Latonia* (Amphibia: Alytidae) from the late Miocene of northern Caucasus (Russia). Palaeobiodiversity and Palaeoenvironments. 1–15.

Syromyatnikova, E., Roček, Z., & van de Velde, S. (2019). New discoveries in the frog *Latonia seyfriedi* (Anura: Alytidae) and their impact on taxonomy of the genus *Latonia*. Paläontologische Zeitschrift. 93(4):669–677.

Szyndlar, Z., 1984. Fossil snakes from Poland. Acta Zoologica Cracoviensa. 28:1–156.

Szyndlar, Z., 1991a. A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos. 47:103–126.

Szyndlar Z. 1991b. A review of Neogene and Quaternary snakes of Central and Eastern Europe. PartII: Natricinae, Elapidae, Viperidae. Estudios Geológicos. 47:237–266.

Szyndlar, Z., 1995. The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscinian Boundary (Neogene). 4. Serpentes (Squamata, Reptilia). Münchner Geowissenschaftliche Abhandlungen (Reihe A) 28:35–39.

Szyndlar, Z., 2012. Early Oligocene to Pliocene Colubridae of Europe: a review. Bulletin de la Société Géologique de France. 183(6):661–681.

Torres-Roig, E., Bailon, S., Bover, P., Alcover, J.A., 2017. An early Pliocene anuran assemblage from Mallorca (Balearic Islands, Western Mediterranean): palaeobiogeographic and palaeoenvironmental implications. Palaeobiodiversity and Palaeoenvironments. 97(2):315–327.

Townsend Jr, V.R., Akin, J.A., Felgenhauer, B.E., Dauphine, J., Kidder, S.A., 1999. Dentition of the ground skink, *Scincella lateralis* (Sauria, Scincidae). Copeia 1999(3):783–788.

Valakos, E.D., Pafilis, P., Sotiropulos, K., Lymberakis, P., Maragou, P., Foufopulos, J., 2008. The amphibians and reptiles of Greece. Frankfurt Contribution to Natural History Volume 32. Edition Chimaira, Frankfurt am Main, 463 pp.

Van Vugt, N., Steenbrink, J., Langereis, C.G., Hilgen, F.J., Meulenkamp, J.E., 1998. Magnetostratigraphy based astronomical tuning of the early Pliocene lacustrine sediments of Ptolemais (NW Greece) and bed-to-bed correlation with the marine record. Earth and Planetary Sciences Letters. 164:535–551.

Vasileiadou, K., Böhme, M., Neubauer, T.A., Georgalis, G.L., Syrides, G.E., Papadopoulou, L., Zouros, N., 2017. Early Miocene gastropod and ectothermic vertebrate remains from the Lesvos Petrified Forest (Greece). Paläontologische Zeitschrift. 91:541–564.

Vasilyan, D., 2019. Fish, amphibian and reptilian assemblage from the middle Miocene locality Gračanica—Bugojno palaeolake, Bosnia and Herzegovina. Palaeobiodiversity and Palaeoenvironments. DOI: 10.1007/s12549-019-00381-8

Venczel, M., 2001. Anurans and squamates from the Lower Pliocene (MN 14) Osztramos1 locality (Northern Hungary). Fragmenta Palaeontologica Hungarica 19:79–90.

Vidal, N., Hedges, S.B., 2005. The phylogeny of squamate reptiles (lizards, snakes, and amphisbaenians) inferred from nine nuclear protein-coding genes. Comptes Rendus Biologies. 328:1000–1008.

Villa, A., Delfino, M., 2018. Fossil lizards and worm lizards (Reptilia, Squamata) from the Neogene and Quaternary of Europe: an overview. Swiss Journal of Palaeontology. 1–35. https://doi.org/10.1007/s13358-018-0172-y

Villa, A., Delfino, M., 2019. A comparative atlas of the skull osteology of European lizards (Reptilia: Squamata). Zoological Journal of the Linnean Society.

Vlachos, E., Delfino, M., 2016. Food for thought: Sub-fossil and fossil chelonian remains from Franchthi Cave and Megalopolis confirm a glacial refuge for *Emys orbicularis* in Peloponnesus (S. Greece). Quaternary Science Reviews. 150:158–171.

Vlachos, E., Kotsakis, T., Delfino, M., 2015. The chelonians from the latest Miocene–Earliest Pliocene localities of Allatini and Pylea (East Thessaloniki, Macedonia, Greece). Comptes Rendus Palevol. 14(3):187–205.

Vlachos, E., Sterli, J., Vasileiadou, K., Syrides, G., 2019. A new species of *Mauremys* (Testudines, Geoemydidae) from the late Miocene–Pliocene of Central Macedonia (northern Greece) with exceptionally wide vertebral scutes. Papers in Palaeontology. 5:177–195.

Zheng, Y., Wiens, J.J., 2016. Combining phylogenomic and supermatrix approaches, and a time-calibrated phylogeny for squamate reptiles (lizards and snakes) based on 52 genes and 4162 species. Molecular phylogenetics and evolution, 94:537–547.

Figure captions:

Fig. 1. Map of Greece, indicating the study area.

Carte de la Grèce, indiquant la zone d'étude.

Fig. 2. *Latonia* sp.: left angular (UU VOR3A 1516) in dorsal (**A**) view; left angular (UU TE1 1504) in dorsal (**B**) view; right maxilla (UU TE1 1502) in lateral (**C**), medial (**D**) and dorsal (**E**) views; right maxilla (UU VOR3 1503) in lateral (**F**), medial (**G**) and dorsal (**H**) views; frontoparietal (UU TE1 1512 [left] and UU TE1 1533 [right]) in dorsal (**I**) and ventral (**J**) views; frontoparietal (UU VOR3A 1518) in dorsal (**K**) and ventral (**L**) views. Scale bars = 1 mm. Abbreviations: cme: crista mandibulae externa; cp: coronoid process; lh: lamina horizontalis; pcp: paracoronoid process; posdep: posterior depression; pc: pars contacta; pp: pterygoid process; spcm: sulcus pro cartilago Meckeli.

Latonia *sp.: angulaire gauche (UU VOR3A 1516) en vue dorsale (**A**) ; angulaire gauche (UU TE1 1504) en vue dorsale (**B**) ; maxillaire droit (UU TE1 1502) en vues latérale (**C**), médiale (**D**) et dorsale (**E**) ; maxillaire droit (UU VOR3 1503) en vues latérale (**F**), médiale (**G**) et dorsale (**H**) ; frontopariétal (UU TE1 1512 [à gauche] et UU TE1 1533 [à droite]) en vues dorsale (**I**) et ventrale (**J**) ; frontopariétal (UU VOR3A 1518) en vues dorsale (**K**) et ventrale (**L**). Barres d'échelle = 1 mm. Abréviations : cme : crista mandibulae externa ; cp : processus coronoïde ; lh : lamina horizontalis ; pcp : processus paracoronoïde ; posdep : dépression postérieure ; pc : pars contacta ; pp : processus ptérygoïde ; spcm : sulcus pro cartilago Meckeli.*

Fig. 3. *Latonia* sp.: atlas (UU VOR3 1506) in dorsal (**A**), ventral (**B**), anterior (**C**) and posterior (**D**) views; atlas (UU VOR3 1521) in dorsal (**E**); ventral (**F**); anterior (**G**) and posterior (**H**) views; trunk vertebra (UU VOR8 1504) in dorsal (**I**), ventral (**J**), anterior (**K**) and posterior (**L**) views; sacral vertebra (UU VOR4 1509) in dorsal (**M**), ventral (**N**), anterior (**O**) and posterior (**P**) views; urostyle (UU VOR3 1501) in anterior (**Q**), dorsal (**R**) and left lateral (**S**) views; urostyle (UU VOR3 1530) in anterior (**T**), dorsal (**U**) and right lateral (**V**) views. Scale bars = 1 mm. Abbreviations: cv: crista ventralis; ivc: intervertebral canal; pt: processus transversus; sp: sacral process.

Latonia *sp.* : *atlas (UU VOR3 1506) en vues dorsale (**A**), ventrale (**B**), antérieure (**C**) et postérieure (**D**) ; atlas (UU VOR3 1521) en vues dorsale (**E**), ventrale (**F**), antérieure (**G**) et postérieure (**H**) ; vertèbre troncale (UU VOR8 1504) en vues dorsale (**I**), ventrale (**J**), antérieure (**K**) et postérieure (**L**) ; vertèbre sacrée (UU VOR4 1509) en vues dorsale (**M**), ventrale (**N**), antérieure (**O**) et postérieure (**P**) ; urostyle (UU VOR3 1501) en vues antérieure (**Q**), dorsale (**R**) et latérale gauche (**S**) ; urostyle (UU VOR3 1530) en vues antérieure (**T**),* *dorsale (**U**) et latérale droite (**V**). Barres d'échelle = 1 mm. Abréviations : cv : crista ventralis ; ivc : canal intervertébral ; pt : processus transversal ; sp : processus sacré.*

Fig. 4. *Latonia* sp.: right scapula (UU NO1 1060) in internal (**A**) and external (**B**) views; coracoid (UU TE3 1527) (**C**); right humerus (UU VOR8 1503) in ventral (**D**), lateral (**E**) and dorsal (**F**) views; left humerus (UU KO1highA 1501) in ventral (**G**), medial (**H**) and dorsal (**I**) views; left ilium (UU VOR3 1502) in lateral (**J**) and medial (**K**) views; left ilium (UU TE1 1509) in lateral (**L**) and medial (**M**) views; left radioulna (UU TE1 1510) in medial view (**N**). Scale bars = 1mm. Abbreviations: ac: acetabulum; cl: crista lateralis; cm: crista medialis; dc: dorsal crest; eu: epicondylus ulnaris; fcv: fossa cubitalis ventralis; hb: humeral ball ; ig: intumescentia glenoidalis; ps: pars suprascapularis; tc: tenuitas cranialis.
Latonia *sp.: scapula droite (UU NO1 1060) en vues interne (**A**) et externe (**B**) ; coracoïde (UU TE3 1527) (**C**) ; humérus droit (UU VOR8 1503) en vues ventrale (**D**), latérale (**E**) et dorsale (**F**) ; humérus gauche (UU KO1highA 1501) en vues ventrale (**G**), médiale (**H**) et dorsale (**I**) ; ilion gauche (UU VOR3 1502) en vues latérale (**J**) et médiale (**K**) ; ilion gauche (UU TE1 1509) en vues latérale (**L**) et médiale (**M**) ; radioulna gauche (UU TE1 1510) en vue médiale. Barres d'échelle = 1 mm. Abréviations : ac : acétabulum ; cl : crista lateralis ; cm : crista medialis ; dc : crête dorsale ; eu : epicondylus ulnaris ; fcv : fossa cubitalis ventralis ; hb : boule humérale ; ig : intumescentia glenoidalis ; ps : pars suprascapularis ; tc : tenuitas cranialis.*

Fig. 5. *Rana* sp.: left humerus (UU NO1 1003) in ventral (**A**), medial (**B**) and dorsal (**C**) views; right humerus (UU TE3 1501) in ventral (**D**), lateral (**E**) and dorsal (**F**) views; left ilium (UU TE2 1501) in lateral (**G**) and medial (**H**) views; right ilium (UU VOR3A 1510) in lateral (**I**) and medial (**J**) views. Ranidae indet.: right angular (UU VOR4 1502) in dorsal (**K**)

and posterior (**L**) views; right angular (UU TE1 1530) in dorsal (**M**) and posterior (**N**) views; left angular (UU VOR2 1513) in dorsal (**O**) views; left maxilla (UU VOR1 1502) in lateral (**P**), medial (**Q**) and dorsal (**R**) views; radioulna (UU TE3 1512) in medial (**S**), lateral (**T**), ventral (**U**) and distal (**V**) views. Scale bars = 1 mm. Abbreviations: ac: acetabulum; cm: crista medialis; cp: coronoid process; crp: crista paracoronoidea; fcv: fossa cubitalis ventralis; fts: fossula tuberis superioris; hb: humeral ball; lh: lamina horizontalis; spcm: sulcus pro cartilago Meckeli; ts: tuber superius.

Rana *sp.: humerus gauche (UU NO1 1003) en vues ventrale (**A**), médiale (**B**) et dorsale (**C**) ; humérus droit (UU TE3 1501) en vues ventrale (**D**), latérale (**E**) et dorsale (**F**) ; ilion gauche (UU TE2 1501) en vues latérale (**G**) et médiale (**H**) ; ilion droit (UU VOR3A 1510) en vues latérale (**I**) et médiale (**J**) ; Ranidae indet.: angulaire droit (UU VOR4 1502) en vues dorsale (**K**) et postérieure (**L**) ; angulaire droit (UU TE1 1530) en vues dorsale (**M**) et postérieure (**N**) ; angulaire gauche (UU VOR2 1513) en vues dorsale (**O**) ; maxillaire gauche (UU VOR1 1502) en vues latérale (**P**), médiale (**Q**) et dorsale (**R**) ; radioulna (UU TE3 1512) en vues médiale (**S**), latérale (**T**), ventrale (**U**) et distale (**V**) ; Barres d'échelle = 1 mm. Abréviations : ac : acétabulum ; cm : crista medialis ; cp : processus coronoïde ; crp : crista paracoronoidea ; fcv : fossa cubitalis ventralis ; fts : fossula tuberis superioris ; hb : boule humérale ; lh : lamina horizontalis ; spcm : sulcus pro cartilago Meckeli ; ts : tuber superius.*

Fig. 6. (non-Bufonidae) Anura indet.: right maxilla (UU TE1 1517) in medial (**A**), lateral (**B**) and dorsal (**C**) views; Anura indet.: sacral vertebra (UU TE1 1519) in dorsal (**D**),ventral (**E**), anterior (**F**), posterior (**G**) and right lateral (**H**) views; urostyle (UU NO1 1048) in anterior (**I**) and dorsal (**J**) views; urostyle (UU TE1 1518) in anterior (**K**) and dorsal (**L**) views. Scale bars = 1 mm.

*Anura (non-Bufonidae) indet.: maxillaire droit (UU TE1 1517) en vues médiale (**A**), latérale (**B**) et dorsale (**C**) ; Anura indet.: vertèbre sacrée (UU TE1 1519) en vues dorsale (**D**), ventrale (**E**), antérieure (**F**), postérieure (**G**) et latérale droite (**H**) ; urostyle (UU NO1 1048) en vues antérieure (**I**) et dorsale (**J**) ; urostyle (UU TE1 1518) en vues antérieure (**K**) et dorsale (**L**). Barres d'échelle = 1 mm.*

Fig. 7. cf. *Testudo* sp.: seventh left peripheral (UU NO1 1071) in external (**A**), visceral (**B**) and ventral (**C**) views. Scale bars = 1 mm.
cf. Testudo *sp.: septième plaque périphérique gauche (UU NO1 1071) en vues externe (**A**), viscérale (**B**) et ventrale (**C**). Barres d'échelle = 1 mm.*

Fig. 8. Testudinoidea indet.: costal (UU VOR1 1507) in external (**A**) and visceral (**B**) views; indeterminate shell fragment (UU TE3 1518) in external (**C**) and visceral (**D**) views; costal (UU VOR2 1501) in external (**E**), visceral (**F**) and lateral (**G**) views; neural (UU VOR3A 1504) in external (**H**), visceral (**I**) and lateral (**J**) views; costal (UU NO1 1001) in external (**K**), visceral (**L**) and proximal (**M**) views; costal (UU NO1 1073) in external (**N**), visceral (**O**) and lateral (**P**) views; distal phalanx (UU VOR3 1526) in lateral (**Q**) view. Scale bars = 1 mm.
*Testudinoidea indet.: plaque costale (UU VOR1 1507) en vues externe (**A**) et viscérale (**B**) ; fragment indéterminé de carapace (UU TE3 1518) en vues externe (**C**) et viscérale (**D**) ; plaque costale (UU VOR2 1501) en vues externe (**E**), viscérale (**F**) et latérale (**G**) ; plaque neurale (UU VOR3A 1504) en vues externe (**H**), viscérale (**I**) et latérale (**J**) ; costale (UU NO1 1001) en vues externe (**K**), viscérale (**L**) et proximale (**M**) ; costale (UU NO1 1073) en vues externe (**N**), viscérale (**O**) et latérale (**P**) ; phalange distale (UU VOR3 1526) en vue latérale (**Q**). Barres d'échelle = 1 mm.*

Fig. 9. Scincidae indet.: right dentary (UU NO1 1036) in dorsal (**A**) and medial (**B**) views; close up of the teeth in lingual view (**C**). Scale bar = 1 mm.

*Scincidae indet.: dentaire droit (UU NO1 1036) en vues dorsale (**A**) et médiale (**B**) ; zoom sur les dents en vue linguale (**C**). Barre d'échelle = 1 mm.*

Fig. 10. Lacertidae indet.: left dentary (UU NO1 1037) in medial (**A**), lateral (**B**) and dorsal (**C**); premaxilla (UU TE1 1515) in right posterolateral (**D**), anterior (**E**) and left lateral (**F**) views; anterior caudal vertebra (UU TE2 1502) in dorsal (**G**), ventral (**H**), anterior (**I**), posterior (**J**) and left lateral (**K**) views. Scale bars = 1 mm. Abbreviations: cd: condyle; ct: cotyle; labf: labial foramen; mf: Meckelian fossa; nc: neural canal; np: nasal process; ns: neural spine; pms: praemaxilla shelf; pz: prezygapophysis; sp: sacral process; sr: subdental ridge.

*Lacertidae indet.: dentaire gauche (UU NO1 1037) en vues médiale (**A**), latérale (**B**) et dorsale (**C**) ; prémaxillaire (UU TE1 1515) en vues postérolatérale droite (**D**), antérieure (**E**) et latérale gauche (**F**) ; vertèbre caudale antérieure (UU TE2 1502) en vues dorsale (**G**), ventrale (**H**), antérieure (**I**), postérieure (**J**) et latérale gauche (**K**). Barres d'échelle = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; labf : foramen labial ; mf : fosse de Meckel ; nc : canal neural ; np : processus nasal ; ns : épine neurale ; pms : plateau prémaxillaire ; pz : prézygapophyse ; sp : processus sacré ; sr : crête subdentaire.*

Fig. 11. Scinciformata or Laterata indet.: right dentary (UU NO1 1016) in dorsal (**A**) and medial (**B**) view; left dentary (UU NO1 1038) in dorsal (**C**) and medial (**D**) views. Scale bars = 1 mm. Abbreviations: ad: angulus distalis; am: angulus mesialis; cdist: crista distalis; ci: carina intercuspidalis; cmes: crista mesialis; labc : labial cusp; lc: lingual cusp; sd: sulcus dentalis; sdo: striae dominantes.

*Scinciformata ou Laterata indet.: dentaire droit (UU NO1 1016) en vues dorsale (**A**) et médiale (**B**) ; dentaire gauche (UU NO1 1038) en vues dorsale (**C**) et médiale (**D**). Barres d'échelle = 1 mm. Abréviations : ad : angulus distalis ; am : angulus mesialis ; cdist : crista distalis ; ci : carina intercuspidalis ; cmes : crista mesialis ; labc : cuspide labiale ; lc : cuspide linguale ; sd : sulcus dentalis ; sdo : striae dominantes.*

Fig. 12. *Anguis* sp.: trunk vertebra (UU NO1 1026) in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**) and left lateral (**E**) views; non-*Anguis* Anguinae indet.: osteoderm (UU KO1highA 1503) in external (**F**) view; Anguidae indet.: caudal vertebra (UU NO1 1027) in dorsal (**G**), ventral (**H**), anterior (**I**), posterior (**J**) and left lateral (**K**) views. Scale bars = 1 mm. Abbreviations: cd: condyle; ct: cotyle; hm: haemapophysis; nc: neural canal; ns: neural spine; ptz: postzygapophysis; pz: prezygapophysis.

Anguis *sp.: vertèbre troncale (UU NO1 1026) en vues dorsale (**A**), ventrale (**B**), antérieure (**C**), postérieure (**D**) et latérale gauche (**E**) ; Anguinae non-*Anguis *indet.: ostéoderme (UU KO1highA 1503) en vue externe (F) ; Anguidae indet.: vertèbre caudale (UU NO1 1027) en vues dorsale (**G**), ventrale (**H**), antérieure (**I**), postérieure (**J**) et latérale gauche (**K**). Barres d'échelle = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; hm : hémapophyse ;nc : canal neural ; ns : épine neurale ; ptz : postzygapophyse ; pz : prézygapophyse.*

Fig. 13. (non-snake) Squamata indet.: trunk vertebra (UU NO1 1010) in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**) and left lateral (**E**) views; cloacal vertebra (UU NO1 1002) in dorsal (**F**), ventral (**G**), anterior (**H**), posterior (**I**) and right lateral (**J**) views. Scale bars = 1 mm. Abbreviations: cd: condyle; ct: cotyle; i: intercentrum; na: neural arch; medf: medial fossa; nc: neural canal; pz: prezygapophysis; scr: subcentral ridge; syn: synapophysis.

*Squamate (non-ophidien) indet.: vertèbre troncale (UU NO1 1010) en vues dorsale (**A**), ventrale (**B**), antérieure (**C**), postérieure (**D**) et latérale gauche (**E**) ; vertèbre cloaquale (UU NO1 1002) en vues dorsale (**F**), ventrale (**G**), antérieure (**H**), postérieure (**I**) et latérale droite (**J**). Barres d'échelle = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; i : intercentrum ; na : arc neural ; medf : fosse médiane ; nc : canal neural ; pz : prézygapophyse ; scr : crête subcentrale ; syn : synapophyse.*

Fig. 14. "Colubrinae" indet.: trunk vertebra (UU NO1 1040) in anterior (**A**), posterior (**B**), dorsal (**C**), ventral (**D**) and left lateral (**E**) views; trunk vertebra (UU NO1 1042) in anterior (**F**), posterior (**G**), dorsal (**H**), ventral (**I**) and left lateral (**J**) views; postcloacal vertebra (UU NO1 1029) in anterior (**K**), posterior (**L**), dorsal (**M**), ventral (**N**) and right lateral (**O**) views; vertebra (UU NO1 1044) in anterior (**P**), posterior (**Q**), dorsal (**R**), ventral (**S**) and left lateral (**T**) views. Scale bars = 1 mm. Abbreviations: cd: condyle; ct: cotyle; d: diapophysis; hk: haemal keel; hm: haemapophysis; lf: lateral foramen; na: neural arch; nc: neural canal; pa: parapophysis; pla: pleurapophysis; pz: prezygapophysis; pzp: prezygapophyseal process; z: zygosphene.

*« Colubrinae » indet.: vertèbre troncale (UU NO1 1040) en vues antérieure (**A**), postérieure (**B**), dorsale (**C**), ventrale (**D**) et latérale gauche (**E**) ; vertèbre troncale (UU NO1 1042) en vues antérieure (**F**), postérieure (**G**), dorsale (**H**), ventrale (**I**) et latérale gauche (**J**) ; vertèbre postcloaquale (UU NO1 1029) en vues antérieure (**K**), postérieure (**L**), dorsale (**M**), ventrale (**N**) et latérale droite (**O**) ; vertèbre (UU NO1 1044) en vues antérieure (**P**), postérieure (**Q**), dorsale (**R**), ventral (**S**) et latérale gauche (**T**). Barres d'échelle = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; d : diapophyse ; hk : quille hémale ; hm : hémapophyse ; lf : foramen latéral ; na : arc neural ; nc : canal neural ; pa : parapophyse ; pla : pleurapophyse ; pz : prézygapophyse ; pzp : processus prézygapophysaire ; z : zygosphène.*

Fig. 15. *Natrix* sp.: trunk vertebra (UU VOR2 1514) in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**) and right lateral (**E**) views; trunk vertebra (UU VOR2 1522) in dorsal (**F**), ventral (**G**), anterior (**H**), posterior (**I**) and right lateral (**J**) views; trunk vertebra (UU VOR3 1513) in dorsal (**K**), ventral (**L**), anterior (**M**), posterior (**N**) and right lateral (**O**) views. Scale bars = 1 mm. Abbreviations: cd: condyle; ct: cotyle; d: diapophysis; hyp: hypapophysis; izr: interzygapophyseal ridge; lf: lateral foramen; mv: margo ventralis; na: neural arch; nc: neural canal; ns: neural spine; pa: parapophysis; ppa: parapophyseal process; ptz: postzygapophysis; pz: prezygapophysis; scf: subcentral foramen; z: zygosphene; za: zygantrum.

Natrix *sp.: vertèbre troncale (UU VOR2 1514) en vues dorsale (**A**), ventrale (**B**), antérieure (**C**), postérieure (**D**) et latérale droite (**E**) ; vertèbre troncale (UU VOR2 1522) en vues dorsale (**F**), ventrale (**G**), antérieure (**H**), postérieure (**I**) et latérale droite (**J**) ; vertèbre troncale (UU VOR3 1513) en vues dorsale (**K**), ventrale (**L**), antérieure (**M**), postérieure (**N**) et latérale droite (**O**). Barres d'échelle = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; d : diapophyse ; hyp : hypapophyse ; izr : crête interzygapophysaire ; lf : foramen latéral ; mv : margo ventralis ; na : arc neural ; nc : canal neural ; ns : épine neurale ; pa ; parapophyse ; ppa : processus parapophysaire ; ptz : postzygapophyse ; pz : prézygapophyse ; scf : foramen subcentral ; z : zygosphène ; za : zygantrum.*

Fig. 16. *Natrix* sp.: trunk vertebra (UU NO1 1070) in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**) and right lateral (**E**) views; trunk vertebra (UU VOR3 1510) in dorsal (**F**), ventral (**G**), anterior (**H**), posterior (**I**) and right lateral (**J**) views; trunk vertebra (UU VOR1 1501) in dorsal (**K**), ventral (**L**), anterior (**M**), posterior (**N**) and right lateral (**O**) views. Scale bars = 1 mm. Abbreviations: cd: condyle; ct: cotyle; hyp: hypapophysis; izr: interzygapophyseal ridge; lf: lateral foramen; mv: margo ventralis; na: neural arch; nc: neural

canal; ns: neural spine; pz: prezygapophysis; scf: subcentral foramen; z: zygosphene; za: zygantrum.

Natrix *sp.: vertèbre troncale (UU NO1 1070) en vues dorsale (**A**), ventrale (**B**), antérieure (**C**), postérieure (**D**) et latérale droite (**E**) ; vertèbre troncale (UU VOR3 1510) en vues dorsale (**F**), ventrale (**G**), antérieure (**H**), postérieure (**I**) et latérale droite (**J**) ; vertèbre troncale (UU VOR1 1501) en vues dorsale (**K**), ventrale (**L**), antérieure (**M**), postérieure (**N**) et latérale droite (**O**). Barres d'échelles = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; hyp : hypapophyse ; izr : crête interzygapophysaire ; lf : foramen latéral ; mv : margo ventralis ; na : arc neural ; nc : canal neural ; ns : épine neurale ; pz : prézygapophyse ; scf ; foramen subcentral ; z : zygosphène ; za : zygantrum.*

Fig. 17. "Natricinae" indet.: trunk vertebra (UU NO1 1064) in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**) and left lateral (**E**) views; trunk vertebra (UU TE2 1511) in dorsal (**F**), ventral (**G**), anterior (**H**), posterior (**I**) and left lateral (**J**) views; trunk vertebra (UU TE1 1514) in dorsal (**K**), ventral (**L**), anterior (**M**), posterior (**N**) and left lateral (**O**) views. Scale bars = 1 mm. Abbreviations: cd: condyle; ct: cotyle; hyp: hypapophysis; izr: interzygapophyseal ridge; lf: lateral foramen; mv: margo ventralis; na: neural arch; nc: neural canal; ns: neural spine; ptz: postzygapophysis; scf: subcentral foramen; z: zygosphene; za: zygantrum.

*« Natricinae » indet.: vertèbre troncale (UU NO1 1064) en vues dorsale (**A**), ventrale (**B**), antérieure (**C**), postérieure (**D**) et latérale gauche (**E**) ; vertèbre troncale (UU TE2 1511) en vues dorsale (**F**), ventrale (**G**), antérieure (**H**), postérieure (**I**) et latérale gauche (**J**) ; vertèbre troncale (UU TE1 1514) en vues dorsale (**K**), ventrale (**L**), antérieure (**M**), postérieure (**N**) et latérale gauche (**O**). Barres d'échelles = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; hyp : hypapophyse ; izr : crête interzygapophysaire ; lf : foramen latéral ; mv : margo ventralis ;*

na : arc neural ; nc : canal neural ; ns : épine neurale ; ptz : postzygapophyse ; scf ; foramen subcentral ; z : zygosphène ; za : zygantrum.

Fig. 18. Colubridae indet.: right pterygoid (UU TE2 1510) in ventral (**A**), dorsal (**B**) and medial view (**C**) views. Scale bar = 1 mm. Abbreviations: ep: ectopterygoid process; ptc: pterygoid crest.

*Colubridae indet.: ptérygoïde droit (UU TE2 1510) en vues ventrale (**A**), dorsale (**B**) et médiale (**C**). Barre d'échelle = 1 mm. Abréviations : ep : processus ectoptérygoïde ; ptc : crête ptérygoïde.*

Fig. 19. Caenophidia indet.: trunk vertebra (UU NO1 1033) in dorsal (**A**), ventral (**B**), anterior (**C**), posterior (**D**) and left lateral (**E**) views; trunk vertebra (UU TE1 1513) in dorsal (**F**), ventral (**G**), anterior (**H**), posterior (**I**) and left lateral (**J**) views; caudal vertebra (UU TE2 1517) in dorsal (**K**), ventral (**L**), anterior (**M**), posterior (**N**) and right lateral (**O**) views. Scale bars = 1mm. Abbreviations: cd: condyle; ct: cotyle; hm: haemapophysis; izr: interzygapophyseal ridge; nc: neural canal; ns: neural spine; pla: pleurapophysis; ptz: postzygapophysis; scf: subcentral foramen; z: zygosphene.

*Caenophidia indet.: vertèbre troncale (UU NO1 1033) en vues dorsale (**A**), ventrale (**B**), antérieure (**C**), postérieure (**D**) et latérale gauche (**E**) ; vertèbre troncale (UU TE1 1513) en vues dorsale (**F**), ventrale (**G**), antérieure (**H**), postérieure (**I**) et latérale gauche (**J**) ; vertèbre caudale (UU TE2 1517) en vues dorsale (**K**), ventrale (**L**), antérieure (**M**), postérieure (**N**) et latérale droite (**O**). Barres d'échelles = 1 mm. Abréviations : cd : condyle ; ct : cotyle ; hm : hémapophyse ; izr : crête interzygapophysaire ; na : arc neural ; nc : canal neural ; ns : épine neurale ; pla : pleurapophyse ; ptz : postzygapophyse ; scf : foramen subcentral ; z : zygosphène.*

Fig. 20. Alethinophidia indet.: trunk vertebra (UU NO1 1012) in ventral (**A**), posterior (**B**) and right lateral (**C**) views. Scale bar = 1mm. Abbreviation: cd: condyle; hk: haemal keel.
*Alethinophidia indet. : vertèbre troncale (UU NO1 1012) en vues ventrale (**A**), postérieure (**B**) et latérale droite (**C**). Barre d'échelle = 1 mm. Abréviation : cd : condyle ; hk : quille hémale.*

Table captions:

Table 1. List of the amphibians and reptiles identified per localities in the Ptolemais Basin (D.D: Data Deficient).
Liste des amphibiens et reptiles identifiés dans chacune des localités du Bassin de Ptolémaïs (D.D : Données manquantes).

Locality	**Age**	**Taxa identified**
Notio 1	3.94 Ma (MN 15)	*Latonia* sp.
		Rana sp.
		Ranidae indet.
		Anura indet.
		cf. *Testudo* sp.
		Testudinoidea indet.

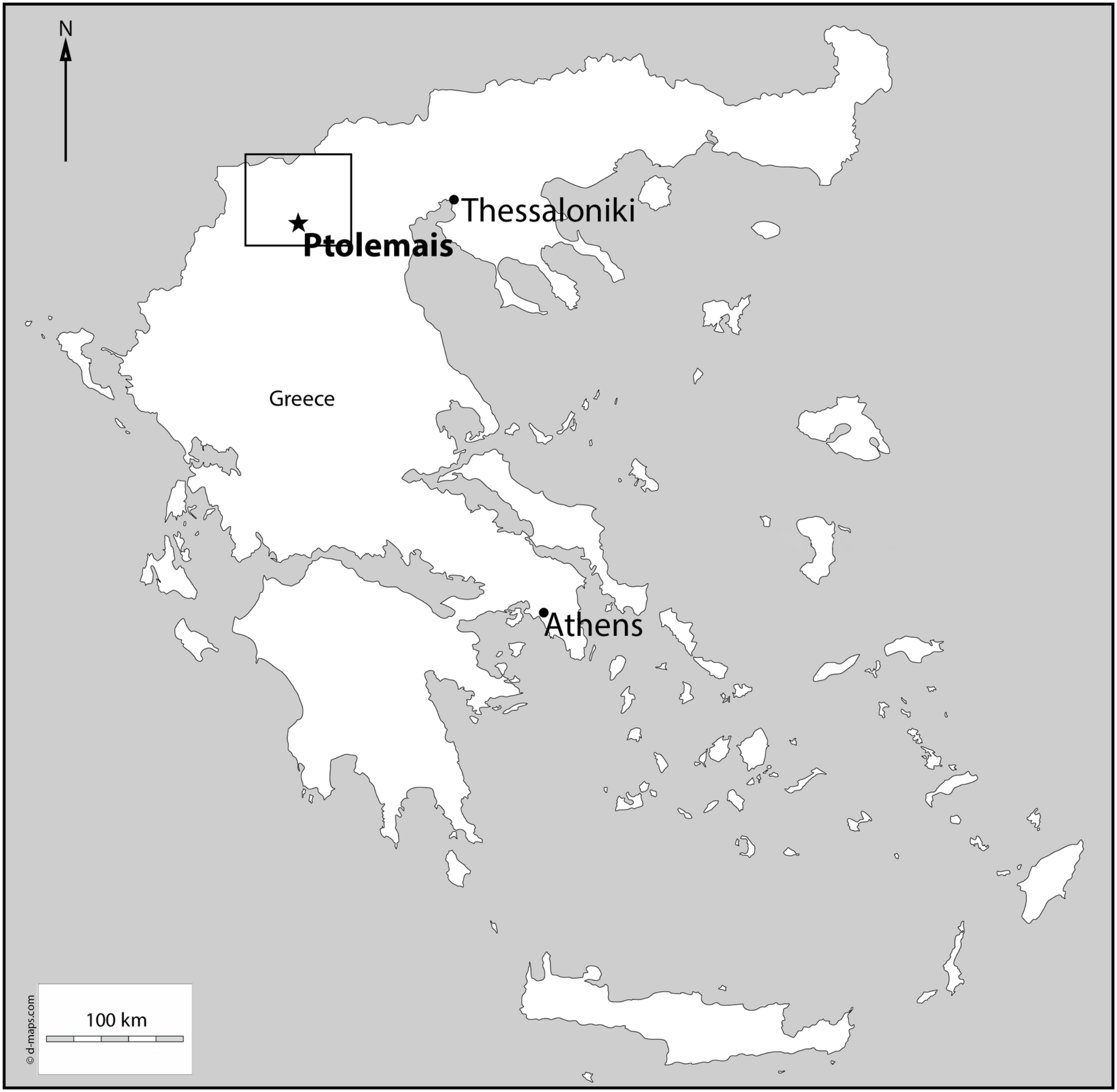
		Scincidae indet. Lacertidae indet. Scinciformata or Laterata indet. *Anguis* sp. Anguidae indet. (non-snake) Squamata indet. "Colubrinae" indet. *Natrix* sp. "Natricinae" indet. Colubridae indet. Caenophidia indet. Alethinophidia indet.
Vorio 8	D.D (MN 15)	*Latonia* sp. Caenophidia indet.
Vorio 4	D.D (MN 15)	*Latonia* sp. Ranidae indet.

		Anura indet.
Vorio 3A	4.9 Ma (MN 15)	*Latonia* sp. *Rana* sp. Ranidae indet. Anura indet. Testudinoidea indet. *Natrix* sp. Caenophidia indet.
Vorio 3	4.9 Ma (MN 15)	*Latonia* sp. Anura indet. Testudinoidea indet. *Natrix* sp. Caenophidia indet.
Vorio 2	D.D (MN 14)	*Latonia* sp. Ranidae indet.

		Anura indet.
		Testudinoidea indet.
		Natrix sp.
Tomea Eksi 3	4.93 – 4.97 Ma (MN 14)	*Latonia* sp.
		Rana sp.
		Ranidae indet.
		Anura indet.
		Testudinoidea indet.
		Caenophidia indet.
Vorio 1	5.04 Ma (MN 14)	*Latonia* sp.
		Ranidae indet.
		Testudinoidea indet
		Natrix sp.

Komanos 1 high A	5.25 Ma (MN 13)	*Latonia* sp. (non-*Anguis*) Anguinae indet.
Komanos 1 low B	5.25 Ma (MN 13)	*Latonia* sp.
Tomea Eksi 2	5.30 – 5.40 Ma (MN 13)	*Latonia* sp. *Rana* sp. Anura indet. Lacertidae indet. Scinciformata or Laterata indet. (non-snake) Squamata indet. “Colubrinae” indet. “Natricinae” indet. Colubridae indet. Caenophidia indet.
Tomea Eksi 1	5.32 – 5.43 Ma (MN 13)	*Latonia* sp.

	Ranidae indet.
	Anura indet.
	Lacertidae indet.
	(non-snake) Squamata indet.
	“Natricinae” indet.
	Caenophidia indet.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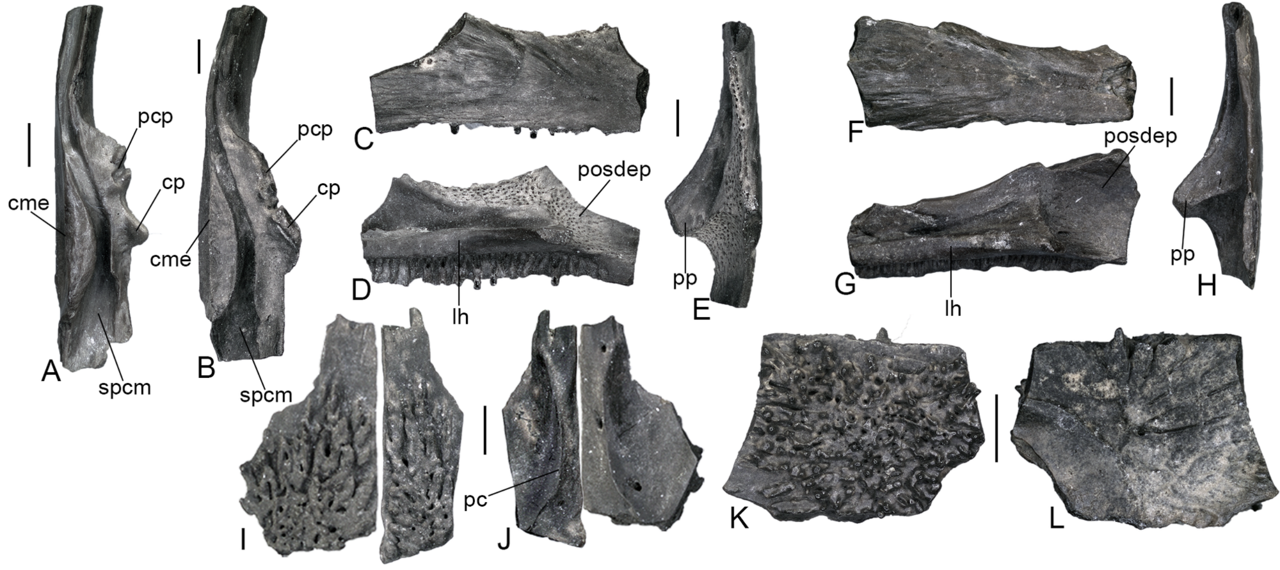

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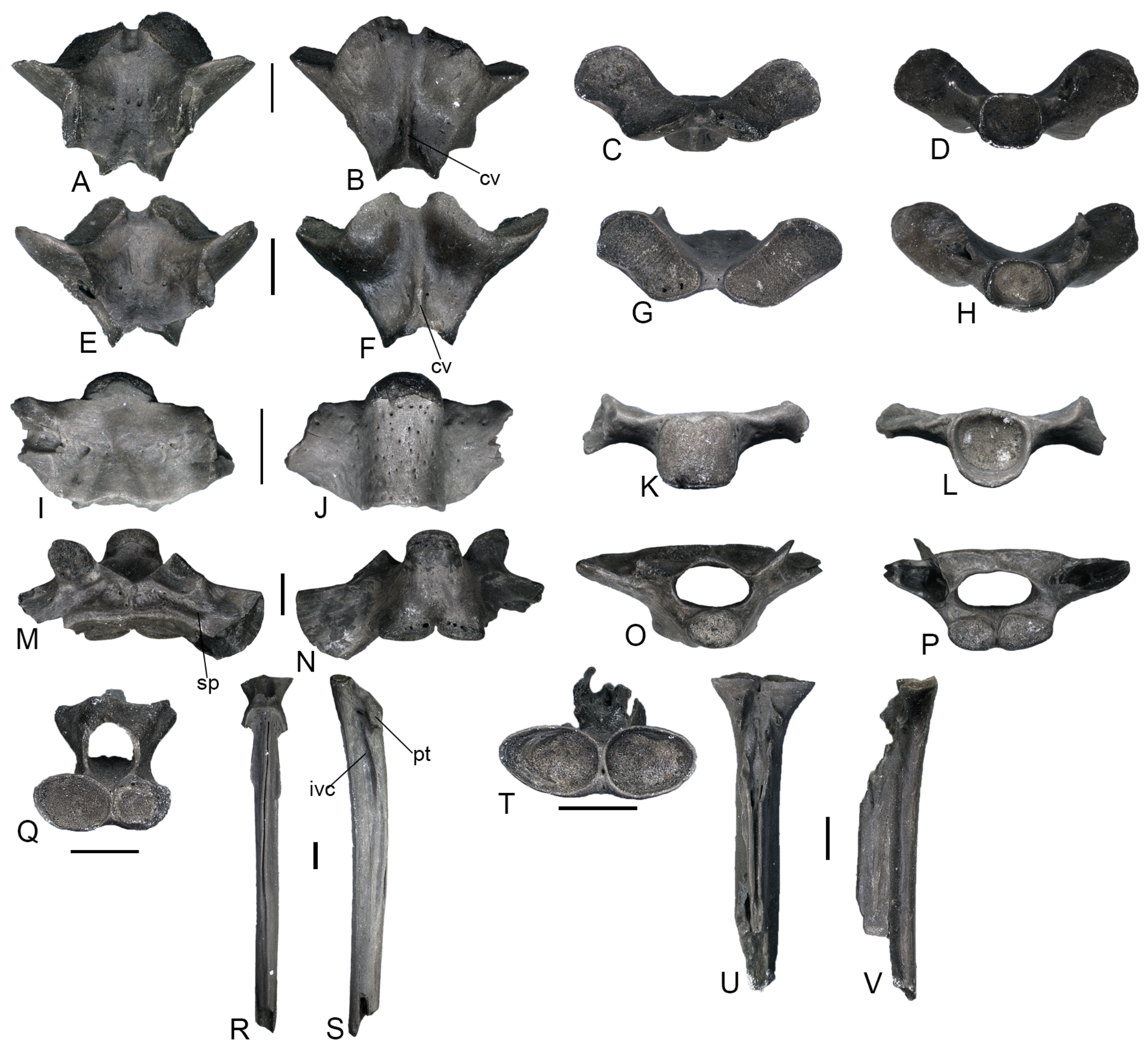
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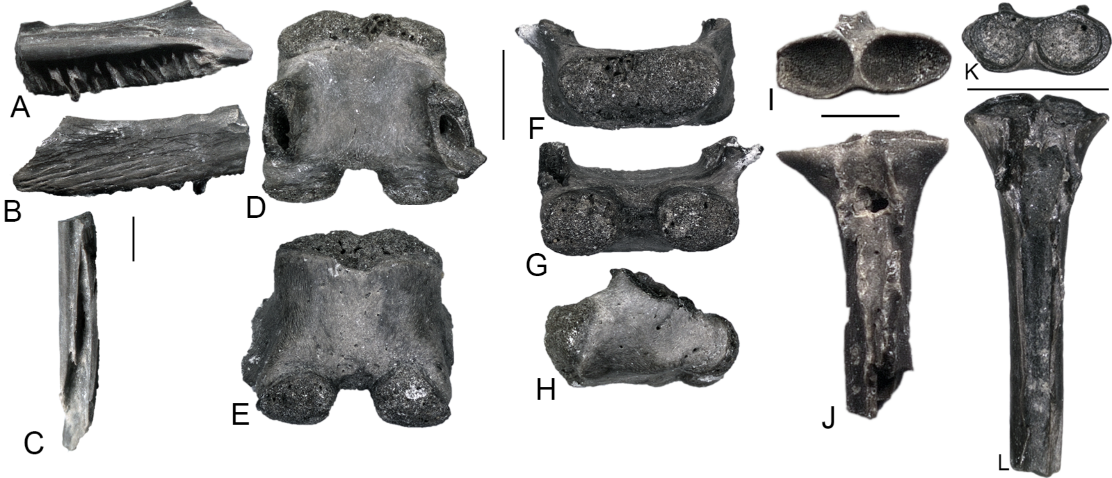
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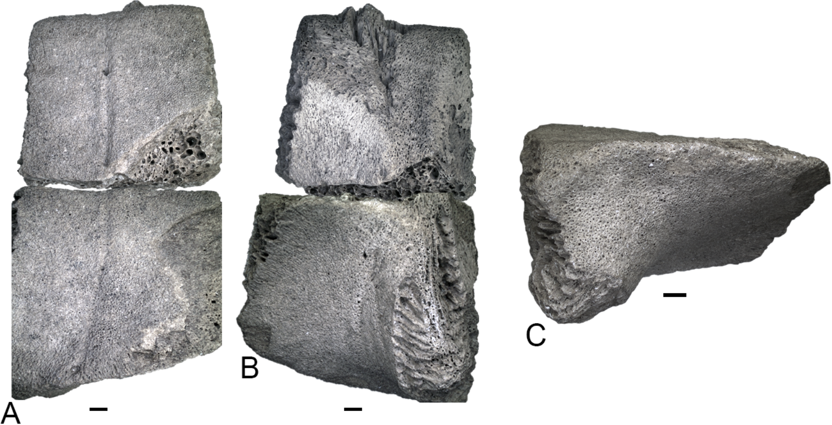
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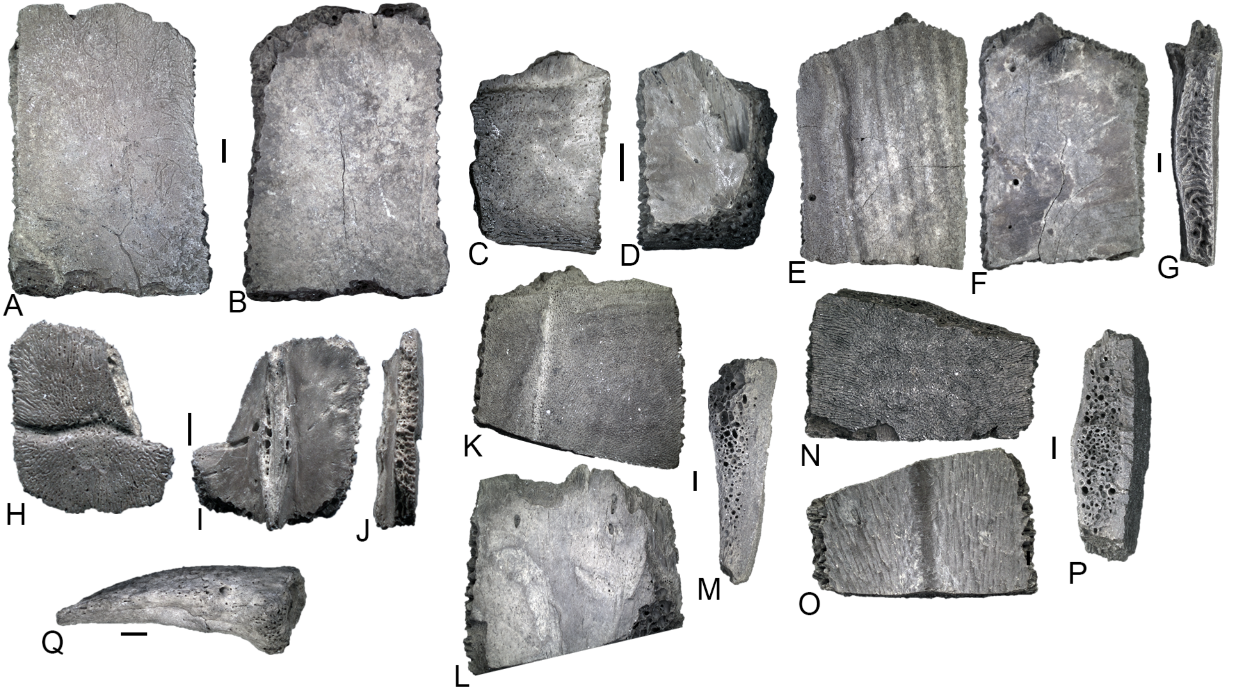
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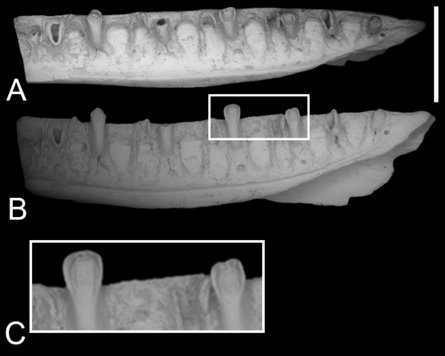
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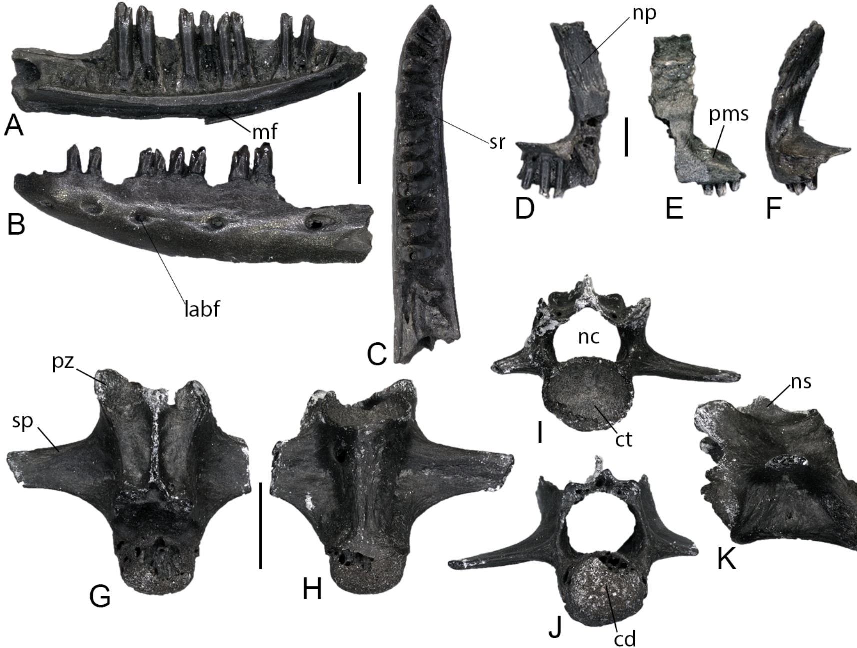

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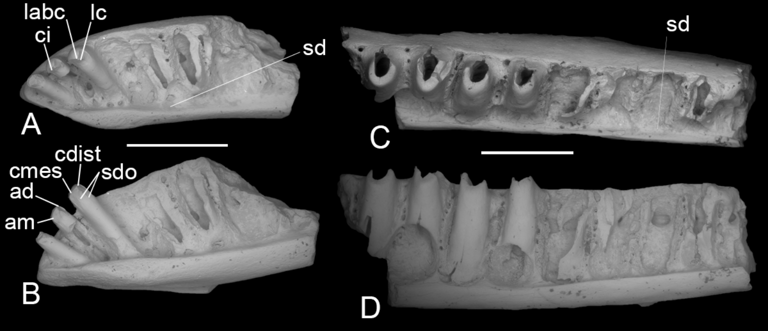

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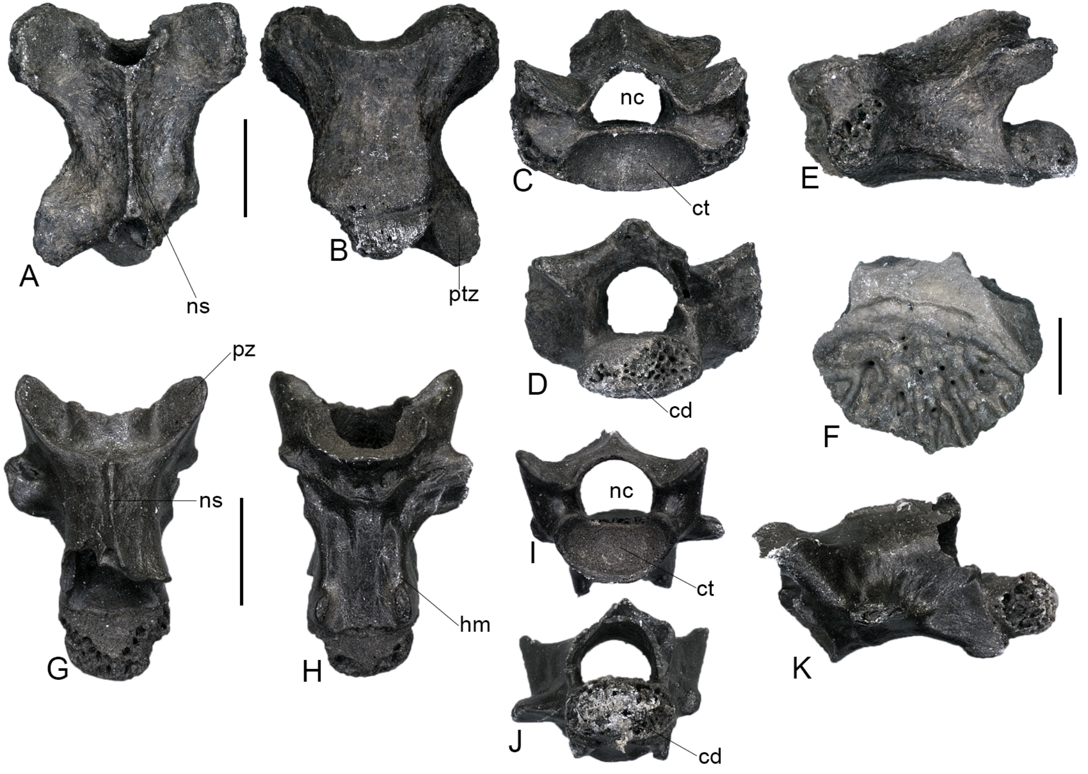
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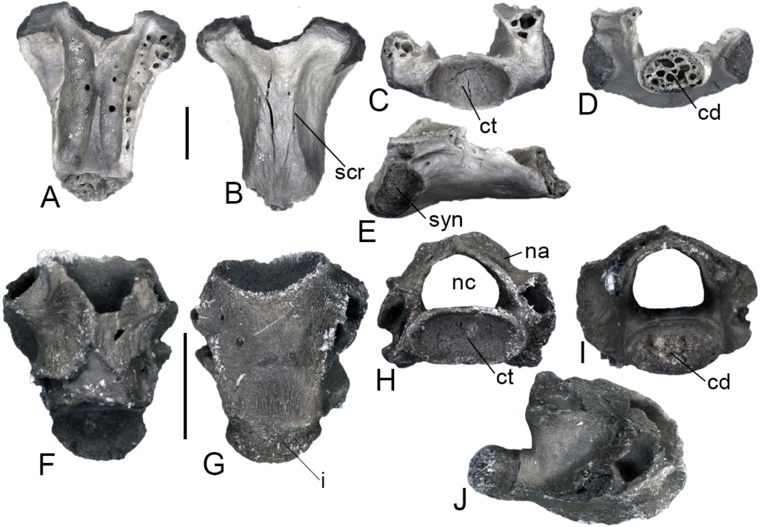
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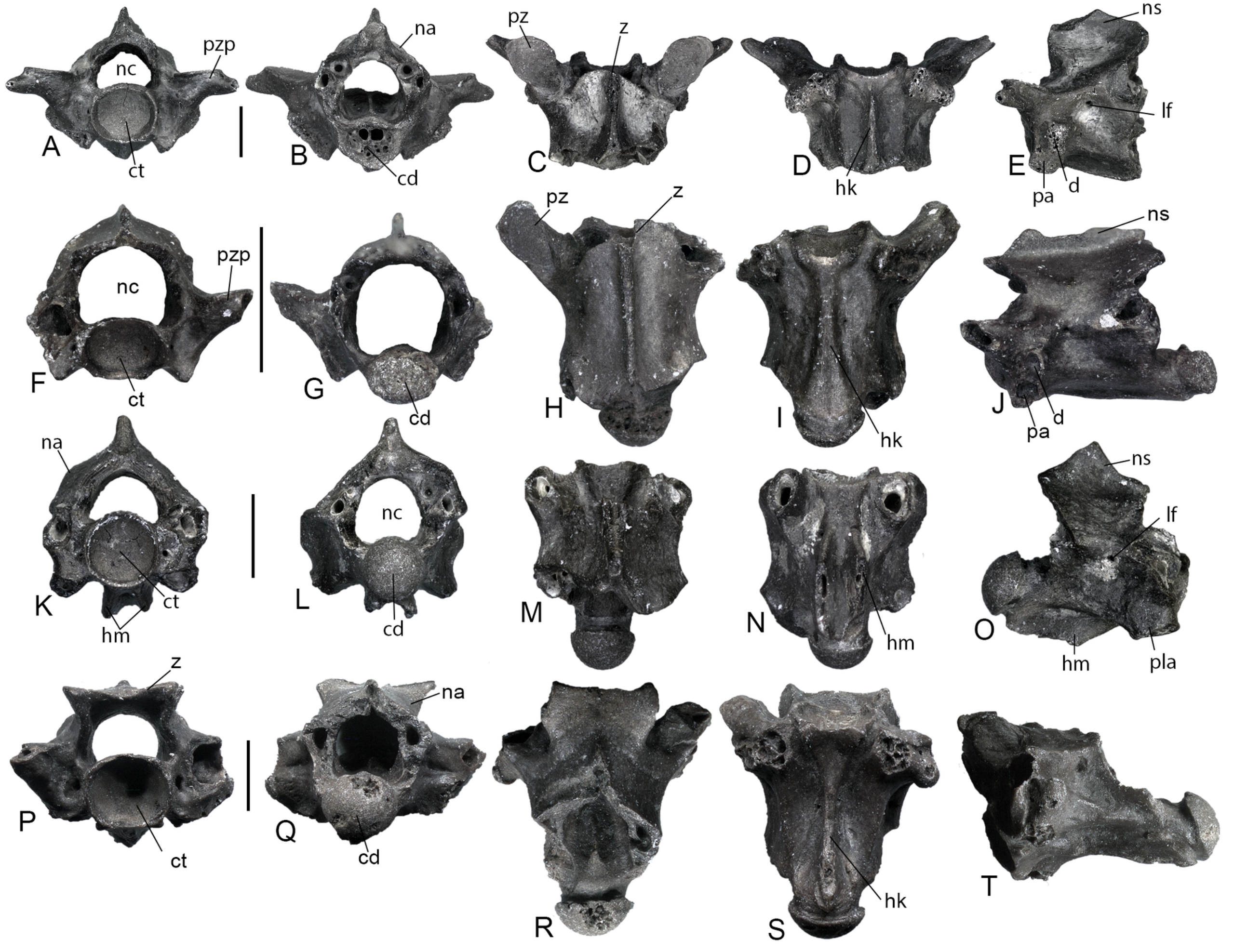

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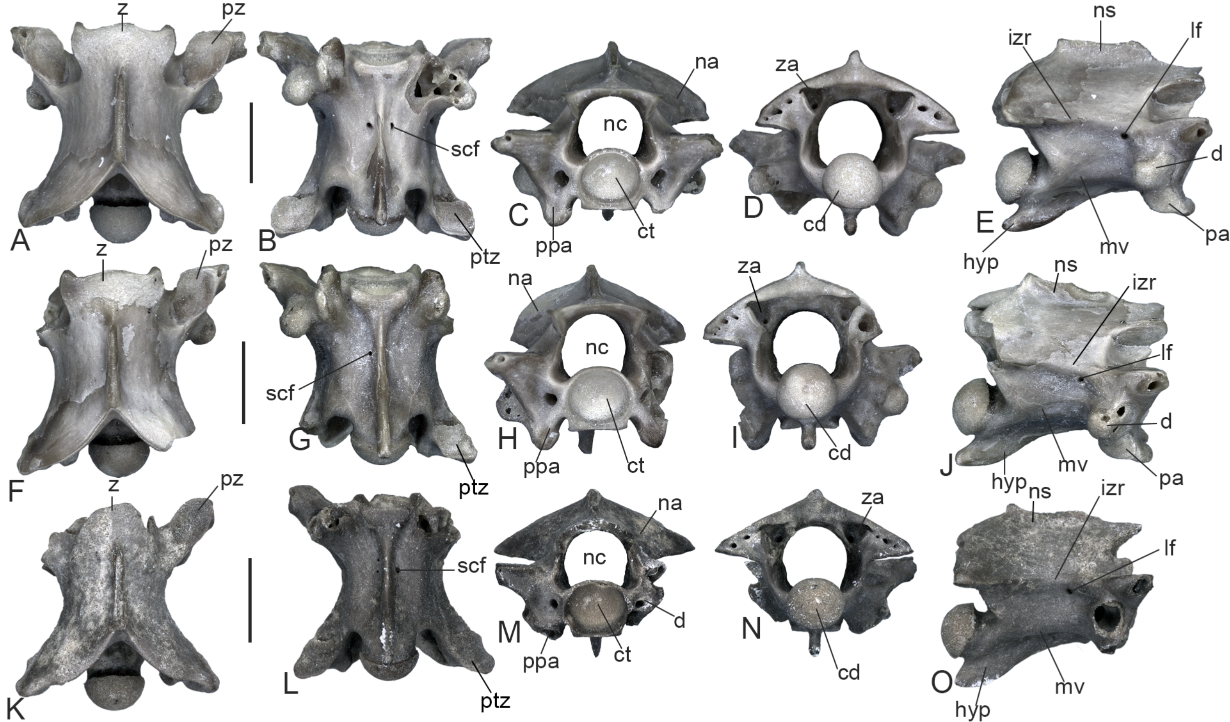
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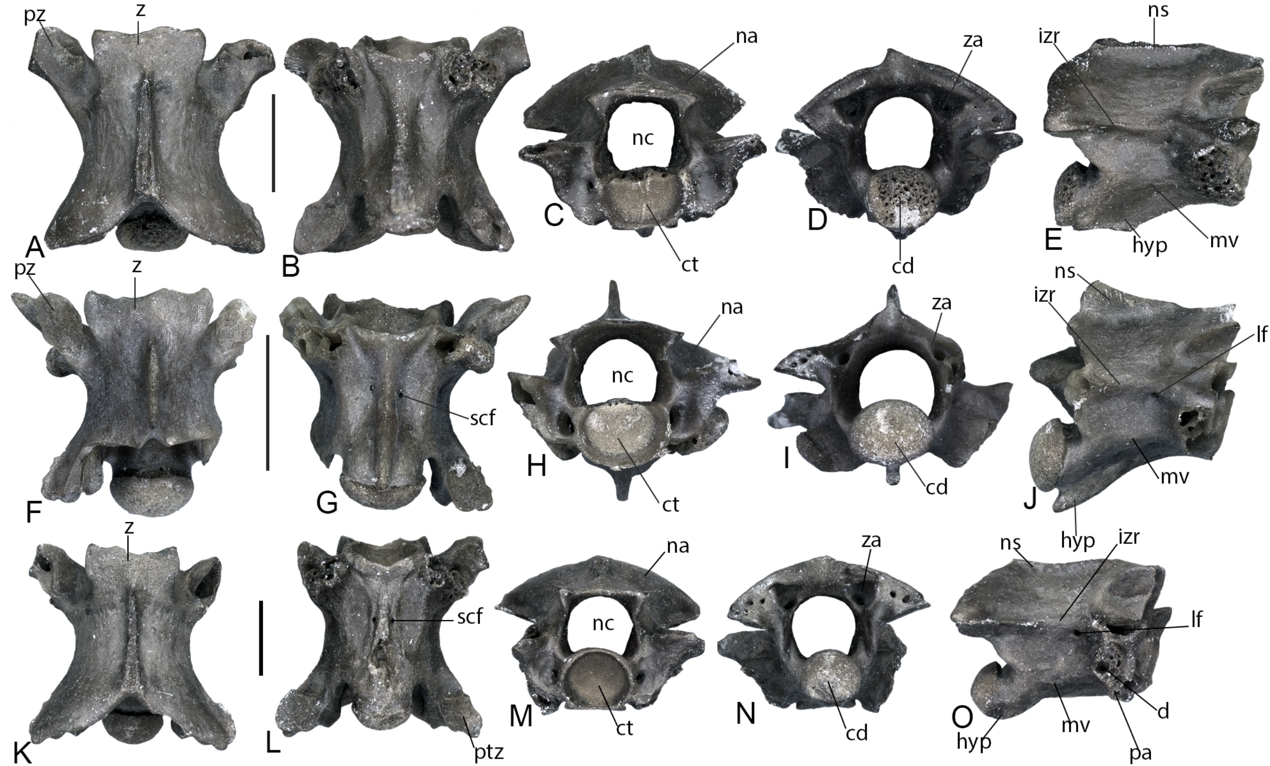

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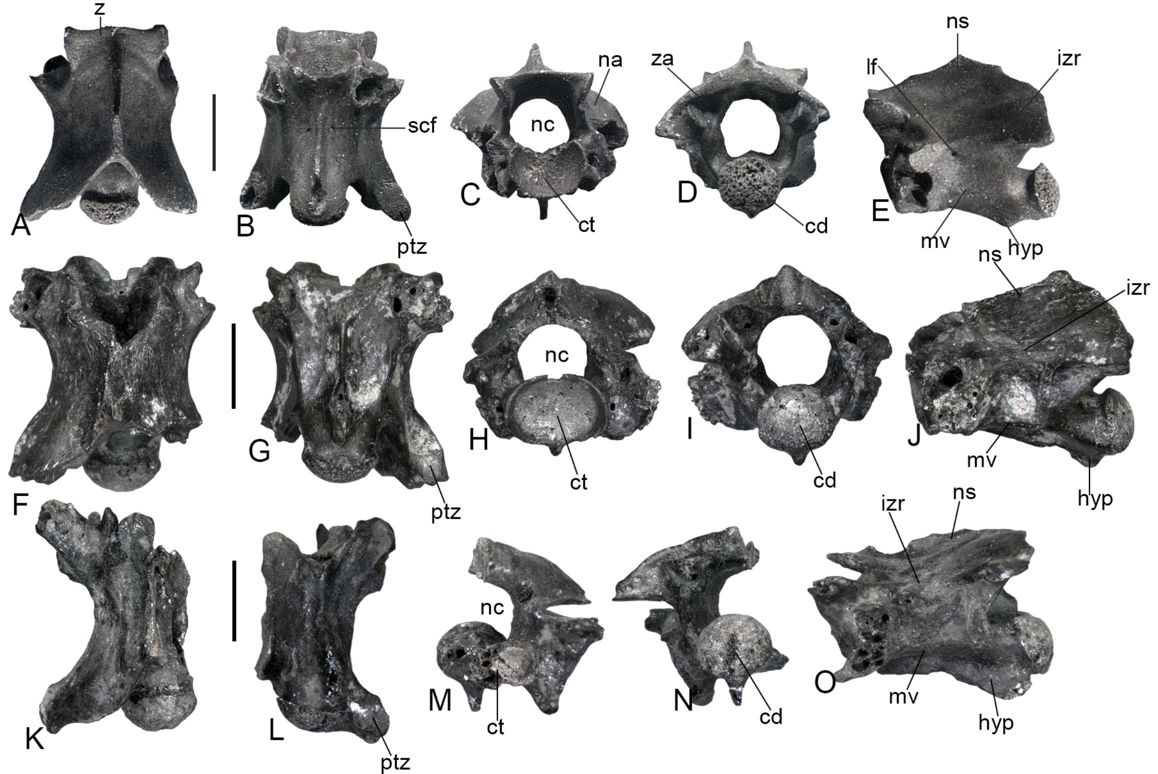
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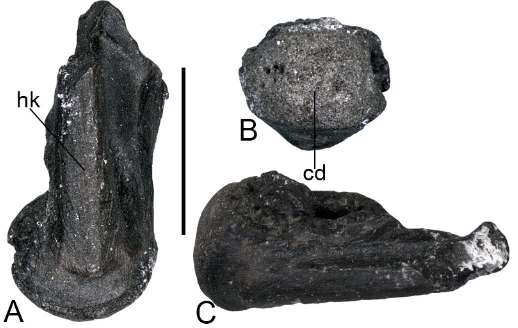
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